Life history characteristics in the sea trout (*Salmo trutta* L.): insights from small catchments in Orkney.

Malcolm Thomson

Thesis submitted for a Doctor of Philosophy
School of Life Sciences
Heriot Watt University
June 2015

ABSTRACT

This thesis investigated life history characteristics in anadromous brown trout (*Salmo trutta* L.) populations inhabiting small coastal streams in the Orkney Islands, Scotland. The main findings were as follows. 1) A total of 36 separate brown trout populations were identified with evidence of anadromy detected in 23. 2) Significant variation in freshwater growth rate occurred even between closely neighbouring populations. 3) Mature resident trout were predominantly male. Their incidence and size between populations was directly related to stream size. 4) Smolt size also varied directly with stream size although age reflected growth rates in each population. Smolts were smaller and younger on average compared to other Scottish populations. 5) Smolts represented both the fastest and slowest growing members in each population studied. Resident mature males exhibited an intermediate growth rate. 6) Some trout de-smolted one year but survived and re-smolted the next year. 7) B-growth in smolts occurred in freshwater and resulted in a significant growth increase between the end of winter and seawater entry. A strong inverse relationship was apparent between individual size at the end of winter and B-growth expression. Information was presented to rekindle the discussion on the presence of a threshold size for seaward migration among anadromous trout.

DEDICATION

To my wonderful family, past, present and future.

ACKOWLEDGEMENTS

First and foremost I would like to thank my wife, Freya, and our children, Ellen and Joe, for their encouragement and support from start to finish. Special thanks also go to my mother, Mary Ann, and sister, Shiona, for the same unwavering support. Thanks also go to a small army of people for helping me during fieldwork. They were, in no particular order, Magnus Spence, Colin Kelday, Dave Cousins, Sue Cousins, Erica Harrap, Willie Smith, Billy Sinclair, John Leask, Duncan Clarke, Paul Sinclair, David Laughton, Alan Macleod, Neil Firth, Colin Kirkpatrick, Neil Macleod, Iain Muir, Duncan MacKenzie, Donald Kirkpatrick, Kevin Heath, Bobby Forbes, Dan Brazier, Dan Wise, Sandy Kerr, Mark Wemyss, Jim Erskine, Raymond Miller and Dave Bottenhorn.

I am grateful to the following people and organizations for providing equipment and/or funding support – the Atlantic Salmon Trust, the Wild Trout Trust, the Orkney Trout Fishing Association, Orkney Builders Ltd., Charlie Dowie, John Young, Ian Richardson Boatbuilder, George Kirkpatrick and Gareth Davies. The design, construction & installation of the Eyrland trap also benefitted from the guidance and help of David Hay (FRS), Andy Walker (FRS), John Webb (AST), Russell Poole (Marine Institute, Ireland), Graham Adamson, Allan Grieve, Geordie Stanger, and Roy Temple. Background data were kindly provided by Katy Beaton (Marine Services, OIC), Peter Cunningham (WRFT), Shona Marshall (WSFT), Eilidh Johnston (SEPA) and Geordie Skea (OTFA). Thank you also to Duncan Clarke for the production of the maps used in this thesis and Mike Bell for providing advice on statistical matters.

I am grateful to all sea trout anglers who reported catches of tagged trout and provided scale samples for analysis. Special thanks go to all landowners in Orkney who provided permission to access burns on their land during fieldwork, particularly to Maurice Groundwater, Stuart Seatter and Jim Stevenson. I am also indebted to my employer Bobby Forbes for supporting me through this process, particularly during fieldwork.

Finally, thanks go to my Supervisor, Dr Alastair Lyndon, for his guidance throughout this thesis.

ACADEMIC REGISTRY
Research Thesis Submission

Name*:*	Malcolm Thomson		
School/PGI:	School of Life Sciences		
Version: *(i.e. First, Resubmission, Final)*	Final	Degree Sought (Award **and** Subject area)	Doctor of Philosophy (Environment)

Declaration

In accordance with the appropriate regulations I hereby submit my thesis and I declare that:

1) the thesis embodies the results of my own work and has been composed by myself
2) where appropriate, I have made acknowledgement of the work of others and have made reference to work carried out in collaboration with other persons
3) the thesis is the correct version of the thesis for submission and is the same version as any electronic versions submitted*.
4) my thesis for the award referred to, deposited in the Heriot-Watt University Library, should be made available for loan or photocopying and be available via the Institutional Repository, subject to such conditions as the Librarian may require
5) I understand that as a student of the University I am required to abide by the Regulations of the University and to conform to its discipline.

* *Please note that it is the responsibility of the candidate to ensure that the correct version of the thesis is submitted.*

Signature of Candidate*:*		Date:	19th June 2015

Submission

Submitted By *(name in capitals):*	
Signature of Individual Submitting:	
Date Submitted:	

For Completion in the Student Service Centre (SSC)

Received in the SSC by *(name in capitals):*			
Method of Submission *(Handed in to SSC; posted through internal/external mail):*			
E-thesis Submitted (**mandatory for final theses)**			
Signature:		Date:	

Please note this form should be bound into the submitted thesis. Updated February 2008, November 2008, February 2009, January 2011

TABLE OF CONTENTS

CHAPTER 6. SMOLTS FROM AN ANADROMOUS BROWN TROUT POPULATION: TRENDS IN FRESHWATER GROWTH AND MIGRATION

CHAPTER 7. UPSTREAM MIGRATION OF SEA TROUT IN THE EYRLAND BURN, ORKNEY, 2007 & 2009

CHAPTER 8. CONCLUSIONS

GLOSSARY

ANOVA:	Analysis of variance
AST:	Atlantic Salmon Trust
cMFL:	Corrected mean fork length
CPUE:	Catch per unit effort
DSFB:	District Salmon Fishery Board
EU:	European Union
FCS:	Fisheries Classification Scheme
FL:	Fork length
K-W:	Kruskall-Walis
LSD:	Least significant difference
MFL:	Mean fork length
MFSTP:	Moray Firth Sea Trout Project
MSA:	Mean smolt age
NASCO:	National Atlantic Salmon Conservation Orgasnisation
NGR:	National grid reference
oFL:	Observed fork length
OIC:	Orkney Islands Council
oMFL:	Observed mean fork length
OS:	Ordnance Survey
OTFA:	Orkney Trout Fishing Association
RAFTS:	Rivers And Fisheries Trusts of Scotland
S1:	Smolts aged one year
S2:	Smolts aged two years
S3:	Smolts aged three years
S4:	Smolts aged four years
SAC:	Special Area of Conservation
SEPA:	Scottish Environment Protection Agency
SFCC:	Scottish Fisheries Co-ordination Centre
SNH:	Scottish Natural Heritage
SPA:	Special Protection Area
SSSI:	Site of Special Scientific Interest
VIE:	Visual implant elastomer
WRFT:	Wester Ross Fisheries Trust
WSFT:	West Sutherland Fisheries Trust

"The islands forming the Orkney and Shetland groups are famous, and justly famous, for their sea-trout; but in their complicity and in their multitude of small waterways, practically all of which carry sea-trout in greater or smaller numbers, provided they afford access to salt water, they present problems requiring more time and personal attention for their elucidation, than I have yet been able to devote to them. The results would be a valuable addition to our knowledge and would almost certainly require a volume to themselves."

G. H. Nall (1930).

CHAPTER 1. REVIEW OF LITERATURE CONCERNING ANADROMOUS BROWN TROUT (SALMO TRUTTA L.)

1.1 Introduction

Sea trout is the term used to describe the anadromous form of the brown trout, *Salmo trutta* (Linneaus, 1758). In recent decades, the profile of the sea trout has increased for various reasons. Salmonids continue to be used as indicators of aquatic health in environmental legislation, *e.g.* the Freshwater Fisheries Directive (European Communities Directive 78/659/EEC[1]). Contemporary legislation such as the EU Water Framework Directive (Directive 2000/60/EC[2]) reinforces this tradition and also highlights the migratory needs of salmonids. The brown trout is a priority species in the UK Local Biodiversity Action Plan and sea trout in particular were recently designated a "priority marine feature" by Scottish Natural Heritage in a process which will ultimately inform the creation of marine protected areas under the Marine Bill (Howson *et al.*, 2012). Sea trout also support recreational fisheries not only throughout their native range in the northeast Atlantic, but in other areas where they have been artificially introduced, for example in New Zealand, Patagonia and the Falkland Islands. In Scotland, many fisheries on the western isles and west coast rely mainly on sea trout and make welcome contributions to remote rural economies (James, 2000). In the Orkney and Shetland Islands sea trout fishing forms part of a uniquely open access trout fishery. Whether this is local custom or remnant of Norse Udal law in the Islands is unclear (Linklater, 2002), but the economic value of brown and sea trout fishing is also appreciated (SQW, 2006). Travelling anglers are considered "high value" tourists whose spend helps to support local jobs and also provides funds through membership and permits to reinvest in conservation and/or management of local fisheries (James, 2000; SQW, 2006). Fisheries management has also attracted considerable investment from private and public sources. In Scotland for example, the creation of fishery trusts over the last 25 years has involved the employment of skilled professionals in the field of fishery research and management, with the core aim of protecting trout and salmon stocks (http://www.rafts.org.uk/about-us/). Scottish Government funding of RAFTS

[1] Official Journal of the European Communities, L 222, 14.8.1978, p. 1.
[2] Official Journal of the European Communities, L 327/1, 22.12.2000, p. 1.

(Rivers and Fisheries Trusts Scotland) between 2008 and 2010 amounted to £1.2 million, which was used to lever in significant additional funds (RAFTS, 2012).

In Scotland particularly, much of this investment has been stimulated by a decline in both salmon and sea trout numbers. Against a gradual long term decline in the national rod and line catch (Marine Scotland, 2012), some individual fisheries have experienced more dramatic reductions in sea trout catches, *e.g.* Loch Maree on the west coast of Scotland (Butler & Walker, 2006). Potential causes of these declines include marine issues such as the spread of parasites from commercial salmon farms, predation by seals and other predators, lack of food and climate change (AST, 2011). Freshwater issues include climate change, pollution, acidification, man-made barriers to migration, predation, competition with alien species, over-fishing and even the effects of stocking hatchery reared trout (Webb *et al.*, 2009). Declines have caused economic loss and reduced biodiversity in aquatic ecosystems (Butler, 2002). As with much aquatic wildlife, sea trout are difficult to observe. Their presence and behaviour is particularly difficult to present to the non-angling public, so declines may go largely un-noticed. While improved sea trout catches have been reported in some areas, *e.g.* Orkney (OTFA, 2010), the general trend of decline across Scotland appears to be continuing, which means that research into sea trout ecology is increasingly necessary. A number of aspects of sea trout ecology remain only partially understood. The Cardiff Sea trout Conference held in 2004 identified a number of key research themes (Milner *et al.*, 2006), which included *inter alia*:

- Management
  - Protection of smaller rivers and streams which provide spawning and nursery habitat for sea trout.

- Science/research
  - Migratory habit: more data is required on genetic and environmental controls.
  - Stock recruitment in a wide range of stream types.
  - Life history strategies in different geographic regions.

This thesis attempts to address these themes in an examination of sea trout populations in the Orkney Islands, off the north coast of Scotland. In his extensive works on sea

trout in the first part of the 20th century, G.H. Nall recognised the productivity and complexity of sea trout populations in Orkney (Nall, 1933). His words, quoted earlier in this thesis, alluded to the value of learning more about these interesting populations. One can readily appreciate the rich opportunities for sea trout research in Orkney, particularly in respect to the themes noted above. Although the islands have several large loch (lacustrine) systems, the coastline is dissected by numerous small burns (streams) that drain directly to the sea. It is certain that some of these support sea trout populations and the identification and characterisation of populations inhabiting these small systems is of interest both from a management and scientific viewpoint as described above. Their relatively small size means that the trout populations which they support can be effectively sampled, so providing excellent case studies in the examination of sea trout ecology. Coincidentally, the possibility of numerous populations existing in a relatively small region means that latitude and the associated effects of varying temperature (Jonsson & L'Abée-Lund, 1993) can be effectively removed as an influence on sea trout ecology, allowing the role of other parameters, *e.g.* stream size, to be assessed. Another incentive for this work is the almost complete absence of data (current or historical) on sea trout in Orkney. The only relevant work is that of Nall (1933), an interesting and detailed piece of work, but limited to two lochs and out of date. This thesis therefore represents a contemporary (and overdue) study of sea trout populations in Orkney and its main scientific aims follow those set out above, *i.e.* to examine the migratory habits, stock recruitment and life history strategies in anadromous brown trout populations, using the opportunities afforded by this unique setting. These scientific aspirations will benefit local efforts to manage and conserve sea trout by providing answers to some basic questions, *e.g.* which burns support sea trout populations? The following sections provide a summary of sea trout ecology, focussing on migratory behaviour, before detailing the specific aims of this thesis.

1.2 Distribution, taxonomy and life cycle

Salmo trutta, the brown trout, was first described by Linnaeus (1758). It is native to the north-eastern area of the Atlantic Ocean, specifically to Europe and its fringes, including Iceland, Russia and mountainous areas of north Africa. It was introduced successfully to other countries in North and South America, Africa, Asia and Australasia, mainly between the mid 1800s and mid 1900s (Elliott, 1994). Brown trout exhibit a range of migratory behaviour which has been described as a "continuum of life

history tactics" (Cucherousset *et al.*, 2005). Some remain within a short distance of their natal home while others migrate downstream to larger rivers or lochs. If access allows, others will migrate further still to brackish estuarine habitats. Finally, some individuals will migrate completely to sea, eschewing their freshwater origins. This last group are termed sea trout. It is important to note that these alternative migratory tactics often co-exist within populations and it is postulated that all individuals within a population might adopt any of the migratory options available to them (Dodson *et al*., 2013). This is termed partial migration and groups showing alternative migratory tactics are often polymorphic, *e.g*. trout which migrate to sea become much larger than trout which reside in freshwater (Jonsson & Jonsson, 1993; Wysujack *et al*., 2009). Partial migration has been observed in many species from the insects to higher vertebrates (Baker, 1978; Biebach 1983; Swingland, 1983; Lundberg, 1985; Berthold, 1991). Other salmonid species to exhibit this tactic include the Arctic char (*Salvelinus alpinus*) (Nordeng, 1961), sockeye salmon (*Oncorrhynchus nerka*) (Foote, 1988) and Atlantic salmon (*Salmo salar*) (Paez *et al*., 2011).

Perhaps unsurprisingly, this polymorphism has resulted in the brown trout having a chequered taxonomic record. Numerous different species under the genus *Salmo* were described in a process, started by Linnaeus, which led to over 50 different sub-species of brown trout being described in the British Isles (Behnke, 1986). This process was also fuelled by the tendency for brown trout body and fin coloration to change depending on their environment (Westley *et al*., 2013). Local examples of these phenomena are provided in Figure 1.1, which shows the classic brown/yellow/olive colour combination with black and red spots, to the silver sea trout with variations between. However, it was Regan (1911) who spliced together these diverting strands by defining the brown trout as a single polytypic species (multiple types under the same species), *Salmo trutta*. This view remains generally accepted and appreciates the plasticity of the brown trout and recognises that the full range of migratory behaviour can occur within as well as between populations (Elliott, 1994). However, it has recently been suggested that in fact, different subspecies of the brown trout may exist which are sympatric but reproductively isolated (Harris & Milner, 2006). Comprehensive reviews of the life cycle of the brown trout can be found elsewhere (Elliott, 1994; Crisp, 2000) and a brief summary is provided here.

1.2.1 Spawning to parr

Spawning takes place in autumn and sees male and female trout pairing up in running water over areas of gravel substrate. The female fish digs a depression in the gravel by lying on her side and flapping her tail, using the upward force generated combined with the flow of water to displace stones downstream. Once a suitably deep pocket has been excavated (the female will test the depth with her anal fin) the female deposits her eggs here, stimulated by the attendant male fish which synchronously fertilises the eggs by the release of sperm (milt) into the water. Subsequently, the female moves further upstream and, repeating the same movements described above, displaces more gravel downstream to fill in the hole and cover the eggs. This process results in a mound of gravel termed a "redd". The eggs incubate within the gravel over the following winter, requiring a steady flow of well oxygenated water to survive. Temperature limits for eggs development have been reported at 0 - 15°C (Elliott, 1981) and 0 - 13°C for 50% of eggs to survive (Crisp 1989). Oxygen requirement for salmonid eggs varies with temperature from 1 mg l^{-1} at 5.5°C, increasing to 7-10 mg l^{-1} at 10-17°C (Davis, 1975; Hamor & Garside 1975, 1976; Turnpenny & Williams 1980; Crisp, 1981). Therefore, over the winter period when water temperatures are low, the incubating eggs are usually supplied with sufficient dissolved oxygen as long as there is an adequate interstitial flow of water through the redd.

Eggs hatch after approximately 440 degree days (Elliott, 1994) but initially remain within the gravel interstices of the redd and rely on their yolk sac for nutrition. This stage, during which the fish is termed the alevin, lasts for approximately 410 degree days and when the yolk sac is consumed, the alevin emerges from the gravel to begin exogenous feeding. This marks the beginning of the fry stage and a period of increased mortality, relative to the egg and alevin stages, as the fry compete for food and space in their nursery environment (Elliott, 1994).

Studies have found that fry can disperse both upstream and downstream from the redd (Elliott, 1994; Moore & Scott, 1988). As the fry develop they enter the parr stage, which is generally accepted as beginning at the age of one year, although Elliott (1994) states that it begins “after a few weeks” from emergence. In any case, it is known that juvenile trout establish feeding territories in during their first summer, which they defend aggressively (Le Cren, 1973). As they grow, their energy demand increases and they increase the size of their territory. Where space and/or food are limited, this can

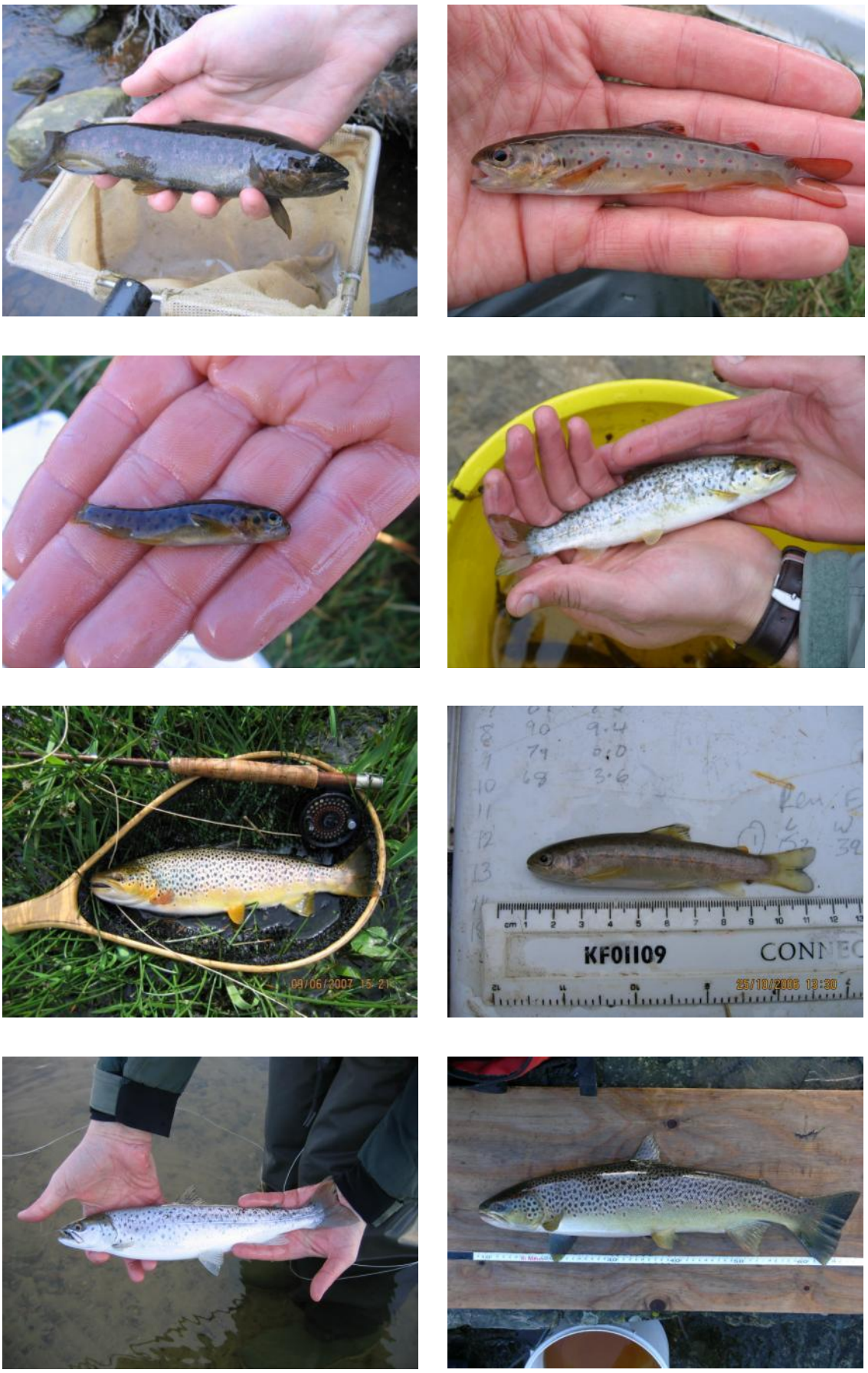


Figure 1.1: A comparison of the different forms of the brown trout sampled in the Orkney Islands by the author between 2004 and 2009.

result in further displacement and/or mortality of parr. Trout are predatory but at the start of exogenous feeding, they are limited to small prey items such as insect larvae. However, as they grow they exploit larger prey and become opportunistic feeders, taking larger terrestrial insects, aquatic insects (larvae through to adults), molluscs and crustaceans (Crisp, 2000). As they grow larger still they may also feed on other fishes, amphibians and small terrestrial mammals (*ibid*). Assuming an adequate food supply, growth is regulated by temperature and occurs between 4 and 19.5°C with the optimum depending on fish size and food intake (Elliott, 1994). As parr increase in size their bodies require more energy to maintain. As this demand approaches the energetic intake then the capacity for further growth is restricted, *i.e*. the growth rate slows down, usually causing the onset of maturity (Jonsson & Jonsson, 1993).

1.2.2 Mature or migrate

Maturity involves the development of reproductive organs in male and female fish which spawn as described earlier, thus completing the life cycle. The development of maturity can be delayed however if the individual can ensure that growth rate does not slow down, typically by migrating into a more productive environment. As described previously, brown trout populations often exhibit partial migration and may shift their niche by employing a range of migratory tactics which involve movements between nursery stream, lochs, estuarine habitats and the sea in order to exploit greater feeding opportunities and hence delay maturation. The factors which are thought to control migratory behaviour are discussed later in section 1.3.

Migration to sea represents the most extreme niche shift for the brown trout which must make significant adaptations in order to cope with the switch from freshwater to marine environment. This involves rigorous physiological and morphological changes in a process termed smoltification, which the lesser migrant forms, *i.e*. those which remain in freshwater, do not experience. A major element of this process is preparation for the transition from freshwater to salt water, which involves *inter alia* a re-organisation of gill function and structure. An increase in the abundance of Na^+, K^+-ATPase enzyme in the gill chloride cells prepares the smolt for marine conditions (and perhaps makes it less tolerant of freshwater conditions), where salts must be actively excreted from the body in order to maintain internal osmotic balance (Tanguy *et al.*, 1994; Finstad *et al.*, 1998). Smolts also take on a highly distinctive silver coloration, achieved by the

secretion of guanine and hypoxanthine from the epithelial cells, and may also lose condition (Hoar, 1988; Titus & Mosegaard, 1992; Byrne *et al.*, 2004). The territorial instincts of the parr dissipate as they form into shoals travelling downstream in spring and by the time they reach the sea they are fully prepared for survival in marine conditions. Environmental variables have a strong influence on this process. Photoperiod and water temperature have been shown to regulate the physiological changes associated with smoltification while water flow and temperature have a strong influence on when smolts actually start moving downstream (Byrne *et al*., 2004; Stefansson *et al*., 2008).

Smolt age varies more–or-less directly with latitude: on average, trout smolt at a younger age in the south than in the north and this most probably a function of how growth varies with temperature. Faster growth therefore results in younger smolts. In France and Spain, brown trout smolt at age one or two (Toledo *et al*., 1993; Euzenat *et al.*, 1999), while in northern Norway, most smolts are between four and six years of age (Jonsson & L'Abée-Lund, 1993). In Scotland, smolts aged one to four years have been reported although two and three year olds are perhaps most common (Nall, 1933; Pratten & Shearer, 1983a; Butler & Walker, 2006). Within populations, faster growing parr tend to migrate at a younger age than slower growing parr, although the slower growers are larger at migration (Økland *et al.*, 1993).

The size at which smolts migrate to sea varies widely in the literature. Fahy (1985) suggested that prospective smolts must reach a threshold size prior to smolting. Rates of survival are reported to increase with smolt size, mainly because of improved osmoregulatory performance (Hoar, 1976). However, Økland *et al.* (1993) discounted the hypothesis of a universal threshold size in anadramous trout populations and suggested instead that smolt size varies within a population and was related to variation in the metabolic rate between cohorts, which is discussed in more detail in section 1.3, below. Between populations, large variations in smolt size are also evident. Jonsson & L'Abée-Lund (1993) reported mean smolt sizes of between 16 and 20cm in Norway and also found that smolt size varied directly with growth rate in freshwater. This might imply that smolt size should decrease with latitude, if growth is related to temperature. Yet in Norway it has also been reported that smolt size increases with increasing latitude (L'Abée-Lund *et al.*, 1989). Smolt size (as well as age) has also been reported to vary directly with stream size. In Norway, Jonsson *et al.* (2001) found smolts of only

6-8cm in length (mean age 1-2 years) in streams with an average annual discharge of 0.05 $m^3 s^{-1}$. This increased to a mean size of 12-16cm (mean age 2-3 years) in streams with discharge of 0.2 $m^3 s^{-1}$ and greater. In Ireland, smolts of up to 27cm (by direct measurement) have been reported for the Owenglena and Invermore systems (Gargan *et al.*, 2006). Therefore, smolt size appears to vary widely but is determined to some degree by the size of the home stream and the growth rate achieved therein.

1.2.3 Marine movement & growth

Sea trout from the North Esk have been found up to 500km away on the west coast of Scotland and across the North Sea, although the bulk of tag returns were from within a 100km radius (Pratten & Shearer, 1983b). Studies in France (Baglinière & Maisse, 1985), Norway (Berg & Berg, 1987) and Ireland also suggest that sea trout undertake much shorter marine migrations in comparison to Atlantic salmon (*Salmo salar*), which generally migrate thousands of miles at sea (Mills, 1989). It is clear however, that sea trout grow rapidly at sea and for a given age, they attain much larger sizes than their non-migratory counterparts. Their marine diet includes fish such as sandeel (*Ammodytes* spp.), sprat (*Sprattus sprattus*), herring (*Clupea harengus*), various crustacea sand polychaete worms (Pemberton, 1976). Growth rates tend to be faster at southern latitudes and slower at northern latitudes, most likely due to sea temperature and associated with this is a tendency for faster growing populations to mature earlier relative to slower growing fishes (Jonsson & L'Abée-Lund, 1993).

1.2.4 Spawning migration & longevity

In spawning, sea trout, like salmon, tend to be faithful to their home river, resulting in genetic differences among different sea trout populations (Ferguson, 2006). Straying rates in the range of 1-3% have been reported (Ferguson, 2006; Jonsson *et al.*, 2004). Genetic studies also highlight instances where straying may be much more common. Sea trout populations inhabiting very small and closely neighbouring streams on the Baltic island of Gotland were found to exhibit high genetic variability, which would not be expected in such small populations if they were reproductively isolated, suggesting flow of genetic material between populations (Laikre *et al.*, 2002). Sea trout returning to freshwater comprise fish which have been at sea for a only a few months (termed "finnock") as well as older larger fish which have been at sea for a year or more and which may have spawned previously. Some finnock may be mature and will spawn

(Caballero *et al.*, 2006), but the majority tend to be immature and may undertake multiple journeys back and forth between the sea and freshwater, often in neighbouring systems (Pratten & Shearer, 1983b). The timing of the return to freshwater varies with the size/age of the fish and with the size of the home river/stream. In large systems, some sea trout return tend to return earlier in the season and these early arriving fish are often the largest and oldest members of the population (Euzenat *et al.*, 2006). In smaller systems, sea trout do not enter until much later in the season. Nall (1933) found that the sea trout returning to the Graemeshall and St Mary's systems in Orkney, both only a few kilometres in length, did so in October and November, shortly before spawning. Unions occur between anadromous males and females, but small resident males can also succeed in fertilising the eggs from larger anadromous females through "sneak" fertilisation at the redd, despite larger male sea trout also being in attendance (Campbell, 1977; Dellefors & Faremo, 1988). Indeed, multiple paternities have been detected in individual batches of sea trout eggs (Garcia-Vasquez *et al.*, 2001). The relative contribution of anadromous and freshwater resident female trout to annual egg deposition can vary. In a small French stream, Charles *et al.* (2004) estimated that resident females contributed the bulk (66%) of eggs annually, while in a small Gotland stream anadromous females were found to deposit 100% of eggs annually (Rubin *et al.*, 2005). After spawning, sea trout move downstream but remain in freshwater for a while to recover from spawning. The time spent in freshwater after spawning also appears to be directly related to river size (Campbell, 1977; Rubin *et al.*, 2005). The resumption of marine feeding helps sea trout to regain condition. However, post-spawning growth rate tends to be significantly less than exhibited prior to maturity (Jonsson, 1985). In a review of research into 102 populations of sea trout across Europe, Jonsson & L'Abée-Lund (1993) found that with increasing latitude, individuals within a population become slower growing but live longer, on average. In northern Norway, sea trout lived for 10 years on average, with the equivalent figure in southern Europe being 5 years. Interestingly however, despite being shorter lived, the proportion of repeat spawners tends to be greater in the shorter lived populations.

1.3 Control of migration

The paragraphs above summarise the life history of the sea trout. Perhaps the most fascinating feature of this life history is the tactic of partial migration whereby individuals within a population demonstrate a range of migratory behaviour. In

particular, the divergence between those trout which remain resident in freshwater and those which migrate fully to sea, and the factors involved in selecting either of these strategies, remains an area of active research. According to Dodson *et al*. (2013) there is ample evidence that these so called alternative migratory tactics (AMTs) co-exist within populations of brown trout and other salmonids, and that all individuals may follow any of the alternative strategies open to them. In salmonids, which AMT selected by an individual is dependent on 'threshold traits' (Hutchings & Myers, 1994; Roff, 1996; West-Eberhard, 2003; Emlen, 2008). Threshold traits exhibit two properties: an underlying 'liability' trait that differs in a continuous fashion and a threshold value which is responsible for the discreetness observed in the phenotypic distribution at a given point in time (*e.g.* freshwater residency versus smolting and emigration) (Falconer & Mackay, 1996). If the value of the liability trait exceeds the threshold value, an individual will choose a different migratory tactic than if the value of the trait is below the threshold. Body size is a commonly used liability trait in salmonid research, *e.g*. Aubin-Horth & Dodson, 2004; Thériault *et al.,* 2007; Piché, Hutchings & Blanchard, 2008) although the application of other physiological traits such as hormone levels, lipid storage and growth efficiency have also been used (McCormick & Naiman, 1984; Hutchings & Myers, 1987; Rowe & Thorpe, 1990; Rowe, Thorpe & Shanks, 1991; Thorpe *et al*., 1998; Forseth *et al*., 1999).

Although commonly used as a liability trait, body size and its relationship to migratory behaviour appears to be highly complex, exemplified in a study by Forseth *et al*. (1999) of a brown trout population in a small Norwegian stream. The authors concluded that "fast growing brown trout migrated earlier and at smaller body size than slower growing individuals", which according to Dodson *et al*. (2013) in a review of AMTs and threshold traits in salmonids, is evidence that fast growth leads to migration. However, further investigation of the Norwegian study shows that migrants aged 0+ and 1+ were actually smaller (in mass) than same aged residents, suggesting instead that slow growth leads to migration! Migrants aged 2+ were larger than same aged residents, which overall, suggests that migratory response to growth may vary with age. One of the main findings of Forseth *et al.* (1999) was that variation in metabolic rate rather than growth *per se* had a strong influence on migration. Those trout which migrated at the youngest age were those which had a faster metabolism and a higher energy demand, so arrived at a growth restriction (or bottleneck) sooner in life than less active non-migrants. In this case it would be more accurate to say that it was fast metabolism and the ensuing

growth restriction, which triggered migration in the youngest age cohorts. Despite their higher energy intake migrants were smaller than same aged non-migrant because they channelled less energy into growth. To some extent, this underpins the traditional theory that nutrient poor systems have a tendency to produce relatively more migrants than nutrient rich systems (Gross *et al.*, 1988; L'Abée-Lund *et al.*, 1990). Variation in metabolic rate might also explain the occurrence of smolts of different ages from within the same population (*e.g*. Økland *et al.,* 1993). Fish which smolt at a younger age are those with higher metabolic rates, so meet a growth bottleneck sooner than those with lower metabolic rates, which form older smolt cohorts. Older smolts have been observed to be larger than younger smolt cohorts a full year before they migrate to sea (Økland *et al.,* 1993). So although they can apparently attain a size at which some trout might migrate to sea, if their metabolic needs are being met as a result of a lower energy demand, then they will not migrate.

Yet fast growth may also promote maturity over migration. Forseth *et al*. (1999) again provide an example of this where among older age cohorts, mature males (no mature females were found) were significantly larger (in mass) than same aged immature fish. In a study of brown trout in a Swedish river, Olsson *et al*. (2006) found that low density and higher growth rates (increase in mass) of fish at an upstream site resulted in a greater rates of residency and maturity in trout relative to a downstream site, where fish density was higher and growth rate slower. These two Scandinavian examples provide some insight into the relationship between growth and the selection of life history choices. It is worth noting however that both studies relate to brown trout populations which are confined to freshwater, with migration consisting of downstream movements from streams/rivers to lake habitats. One of the few studies to deal with a truly anadromous population of brown trout is that of Jonsson (1985) who reported growth rates of resident mature trout to be within the range exhibited by migratory (sea) trout in the Vangsvatnet Lake, Norway, *i.e.* slower than fast growing young smolts but faster than slow growing older smolts. This final example emphasizes, if it was necessary, the complexity of the relationship between body size and choice of migratory tactic.

It is important to note at this point that migration can be the end-point for both fast and slow growing individuals. This has been noted in several studies on anadromous brown trout populations (Jonsson, 1985, Økland *et al.,* 1993; Bohlin *et al*., 1993, 1996), which lends support to the theory that a threshold size triggers migration in salmonids (Elson,

1957; Fahy, 1985). But what evidence is there for a specific threshold value in body size which influences migratory choices, bearing in mind the complexity of this relationship? Thresholds sizes for migration have been suggested in salmonids (Aubin-Dorth & Dodson, 2004; Thériault *et al*., 2007; Piché *et al*., 2008). Multiple thresholds have been described for Atlantic salmon that operate over consecutive years, providing alternative developmental pathways which end in either migration to sea (via a fast and slow pathway) or freshwater residency and maturity (Paez *et al*., 2011; Rossignol *et al*., 2011) . Interestingly, in these studies the youngest and oldest salmon smolts were those which exhibited the fastest and slowest growth rates, respectively, while those showing intermediate growth became mature in freshwater. A similar finding was made in a study of an anadramous brown trout population, mentioned earlier (Jonsson, 1985). Fahy (1985) suggested that *Salmo trutta* conforms to similar size threshold to achieve migration to sea as postulated for *Salmo salar* by Elson (1957), whereby individuals which reach a size of 10cm by autumn will smolt and migrate to sea the following year. This hypothesis (for *Salmo trutta*) was refuted by Økland *et al.* (1993) and the subject appears to have attracted scant attention in the literature since.

Other factors which influence the choice of migratory tactic include environmental factors, fish gender and genetics. Environmental factors such as fish density, competition for food, habitat availability, food availability, water temperature and predation are known in influence rates of growth (Armstrong *et al*., 2003). This was demonstrated by Olsson *et al*. (2006) who transplanted wild brown trout between an upstream site, where trout were fast growing and showed a tendency towards residency, and a downstream site, where they were slower growing and tended towards migration. Transplanted fish changed their behaviour to reflect that of the new habitat. Wysujack *et al*. (2008) demonstrated in hatchery conditions that brown trout from the same gene pool exhibited a greater tendency towards migratory tactics when raised on a lower food ration. Environmental gradients may also indirectly affect growth patterns and hence migratory behaviour. On average, smolt age in brown trout populations increases with increasing latitude due to the suppressive effect of decreasing water temperature on growth (Toledo *et al*., 1993; Euzenat *et al.*, 1999). The rate of anadromy in trout populations has been found to decrease as the altitude of the spawning area increased (Bohlin *et al.*, 2001). It is suggested that this could represent a situation where the potentially high risks & costs of a migratory strategy is rejected in favour of a less risky resident tactic.

There is also a clear difference in the migratory behaviour of male and female brown trout. Numerous studies show a propensity among males to reside and mature in their natal streams, in contrast to females which tend to migrate to more productive habitats before returning later as larger, mature fishes (Campbell, 1977; Jonsson, 1985; Forseth *et al.*, 1999; Jonsson *et al.*, 2001). It is thought that this preference for migration is an adaptive strategy to increase reproductive success, as by moving to more productive habitats female trout can grow larger. This brings a number of advantages, chiefly that fecundity (egg output) is increased. For males however, reproductive success does not seem so closely linked with size. Small resident males can successfully fertilise eggs of both from resident females as well as from larger migrant females, through direct courting or "sneak" fertilisation as described above. Precocious male Atlantic salmon, have been found to fertilise up to 86% of the eggs in a single redd constructed by an anadromous female (Garcia-Vasquez *et al*., 2001) but there are no similar estimates for brown trout. Incidentally, it has been reported that brown trout which mature in freshwater can subsequently smolt and migrate to sea before returning to spawn (L'Abée-Lund *et al.*, 1990; Titus & Mosegaard, 1992), although others suggest that few if any resident male brown trout smolt after reaching maturity in freshwater (Dellefors & Faremo, 1988).

While the adoption of AMTs do not generally result in genetic divergence (Dodson *et al*. (2013), genetics do influence how individuals and populations respond to the triggers thought to be involved in salmonid migration. Variation in liability traits such as growth and metabolic rate are to some extent genetically determined and are consequently heritable, thus promoting diversity in migratory choice over generations. For example, a laboratory study on Atlantic salmon found significant heritability in the incidence of juvenile salmon in lower and upper modal size groups and in the threshold body size which marked the boundary between the two groups (Páez *et al*., 2011). Another laboratory study involving Atlantic salmon found that the incidence of precocious male maturity was a heritable trait which varied between individuals in the same population and between different populations (Piché *et al*., 2008). Variation in sensitivity to the hormones which are involved in the regulation of salmonid migration, such as growth hormone and growth-hormone-releasing hormone might also have a heritable trait (Dodson *et al*., 2013). In summary, the control of migration in brown trout appears to be "under genetic control with fine tuning by the environment" (Jonsson & Jonsson, 2006), the final result varying both within and among populations.

Therefore, questions remain concerning the migratory behaviour of salmonid species and continued investigation is necessary, perhaps even more so in relation to the brown trout, which appears to have been the focus of less research relative to other salmonid species.

1.4 Aims

The research aims of this thesis revolved around the scientific objectives formulated in the 2004 Sea Trout Symposium, which included further research into migratory habits, populations inhabiting different stream types and life history strategies in different geographic regions. Questions from more contemporary research relating to the control of migration were also considered. The Orkney Islands presented the ideal context for these investigations, having been the setting for work by G. H. Nall in the past, and where it is thought numerous populations of sea trout exist in the many small streams which intersect its coastline. One of the first and most important aims was to address the dearth of contemporary data on sea trout populations in the area, and so provide a framework for more detailed research to follow. Therefore, the specific aims of this thesis were:

- To determine which of Orkney's numerous streams support anadromous brown trout and to provide a broad comparison of features such as growth, smolt size & age and the occurrence of mature resident fish (Chapter 3);
- To carry out a detailed examination of freshwater growth patterns in four anadromous trout populations and determine whether factors such as stream size and juvenile density influence growth in juvenile and mature resident trout (Chapter 4).
- To examine smolting trout from the same four populations and test the hypothesis that factors such as pre-migratory growth rate and stream size influence the size and age of smolts at the time of migration (Chapter 5);
- To examine the smolt migration from the Eyrland Burn, located on mainland Orkney, over a seven year period in order to determine rates of annual productivity in a burn of this size and answer questions such as what factors are responsible for initiating smolt migration, do smolt age/size characteristics change through the migration period, what is the incidence of de-smolting fish, does a critical body size play a role in the smolting process and what role does B-growth play in determining smolt size at seawater entry (Chapter 6).

- To examine the return migration of sea trout to the Eyrland burn and quantify the size of the spawning population and determine what factors control the upstream movement of sea trout, the sex ratio of returning sea trout, the smolt age and marine growth of surviving fish and whether or not the occurrence of B-growth is significant when adult fish data are used to determine previous life history events (Chapter 7).

In working to achieve these aims it is also hoped that some valuable practical knowledge can be obtained which will prove useful to the conservation of sea trout in the Orkney Islands.

CHAPTER 2. STUDY AREA AND METHODS

2.1 Study area

The Orkney Islands comprise an archipelago of approximately 70 islands located off the north coast of Scotland at a latitude of 59° North (Figure 2.1). They lie at a distinct marine junction with the North Sea to the east and the Atlantic Ocean to the west. The movement of water between these two areas results in strong tidal flows around the islands. The channel between Orkney and the Scottish mainland, known as the Pentland Firth, is a particularly energetic area with tides reaching in excess of 10 knots in places (UKHO, 2012). Orkney is also exposed to significant wave action from the Atlantic Ocean, particularly along its west coast. Areas of shelter also exist. Scapa Flow is a large area of sea protected on nearly all sides by islands which, with its deep water, provided a famous anchorage for the British Navy in two World Wars. Indeed, it was during the Second World War that its eastern approaches were closed off by the construction of the Churchill Barriers, which reduced tidal velocities in the Flow even further. These extremes of exposure have combined to have a significant effect on the history, culture and environment of the Orkney Islands. The following description of Orkney's environment is taken mostly from Berry (1985).

The climate of Orkney also has a major effect on its character. Monthly climatic data are provided in Table 2.1. Described as "hyperoceanic" along with the Western and Shetland Islands and areas of north-west Scotland, Orkney is warmed to some extent by the Gulf Stream, although this is more evident in the winter months when daily average temperatures are similar to those in Edinburgh and only 1°C less than London. Summers temperatures are somewhat cooler than the rest of the UK. The overall effect is that Orkney experiences less seasonal variation in temperature compared to southern areas of the UK. This also holds for sea temperature with a range approximately between 5°C in February and 13°C in July. In terms of precipitation, Orkney lies mid-table, experiencing around 1000mm of rain annually, which is more than eastern parts of the UK but less than many western parts. The driest months are May and June. Gales may occur at any time of year although are most frequent in the winter months.

The Orkney land mass is based predominantly on Old Red Sandstone, formed around 380 million years ago. This sandstone is punctured in places, *e.g.* Stromness, by

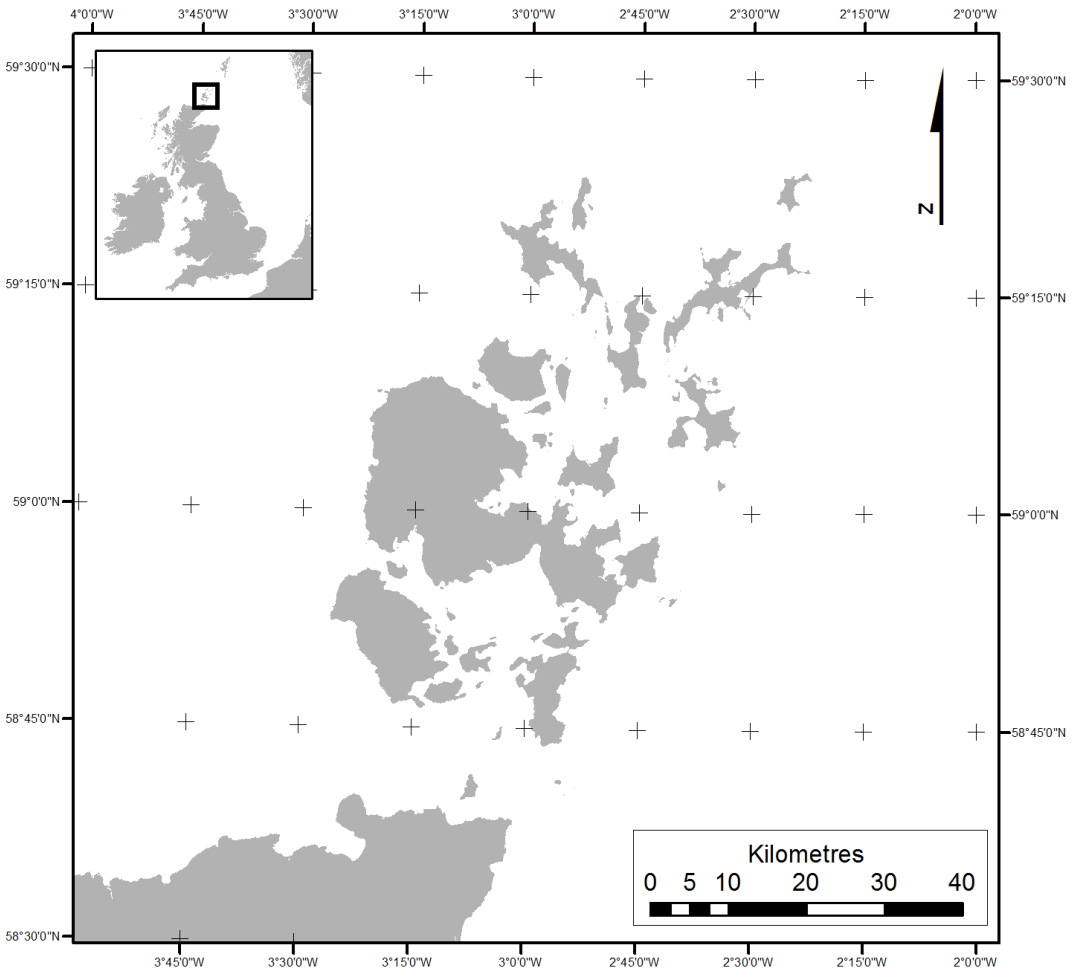


Figure 2.1: The Orkney Islands form an archipelago located off the north coast of Scotland.

underlying igneous rock, composed mainly of granite. The soils above comprise a sandy, boulder clay and the land is generally low lying, gently undulating and fertile. Consequently it is suitable for agriculture, which has had a major impact on the Orkney landscape. Evidence of primitive farming dates to 3000 BC but the modern pattern of agriculture developed from the 1800s, with a series of events which facilitated land "improvement" and greatly increased productivity. Amongst other things this involved land drainage to bring wet land into agricultural use, beginning a process whereby natural watercourses were altered to increase their drainage capacity. This process continued gradually through the early 1900s but accelerated greatly in the years after World War Two, when huge areas of hill ground were converted to crop production, fuelled by agricultural subsidy. This necessitated further drainage and the period saw significant changes to Orkney's many burns, which were straightened and deepened to

accommodate the flow of water from the land. The Orkney countryside is now dominated by agricultural activity. MLURI (1993) estimated that improved and rough grassland accounted for 63% of the land area of the islands. Areas of unfarmed land comprise heather moorland, for example, the upland areas of the west mainland and on the island of Hoy, both of which are designated special protection areas (SPAs) under the EU Bird's Directive. Land "improvement" has virtually ceased and grants are now available for landowners to allow land to revert to a more natural state.

The landscape is drained by numerous lochs and burns. The vast majority are alkaline in character, a result of soil type and geology (Duncan *et al.,* 1992). Nutrient levels are moderately high as a result of agricultural practices, particularly the application of fertilisers to the land. Most lochs are low lying and several have been classed as either mesotrophic or eutrophic, *e.g.* the lochs of Harray and Boardhouse. Upland lochs, of which there are only a handful, are less nutrient rich and usually acidic due to the surrounding peatland, *e.g.* the lochs of Hoglinns and Heldale in Hoy (Charter & van Houten, 1989). The largest freshwater system is located on the west mainland of Orkney and comprises both the lochs of Stenness (SAC) and Harray (SSSI) with a combined catchment of approximately 126km^2 (Bennion *et al*., 2002). The other main lochs include Boardhouse, Hundland, Swanney & Kirbister, also in the west mainland.

There are no rivers as such in Orkney and although there are some quite large burns, most are only a few miles long. The Durkadale burn in Orkney's west mainland has the largest catchment area at 19km^2. The vast majority of burns have catchments of less than 10km^2, as identified recently in the river basin planning process carried out in Orkney under the Water Framework Directive (SEPA, 2014). While some burns are associated with lochs, many drain directly to the sea. As described above, many burns have been straightened and deepened to facilitate land drainage. Harbinson (1998) estimated that of the combined length of the main burns flowing into Scapa Flow, 68% had been canalised. In general, this is mostly evident where agriculture is intense, like the Orkney mainland. In contrast, the burns on the island of Hoy generally run a natural course through a landscape which is less suitable for agriculture.

The aquatic flora and fauna of Orkney have been studied on various occasions. Numerous species of pondweed occur in the Loch of Harray which forms part of its SSSI designation. Some particularly rare stonewort species have been recorded in the

Table 2.1: Climatic data reproduced from the Orkney Economic Review 2011 published by the Orkney Islands Council. Sources: 2010 data: Loch of Hundland climate station, 10 year average, period 2000 – 2009: Loch of Hundland climate station, 50 year average: Kirkwall Airport data 1950-2000

Month	**Mean MAXIMUM Temp (°C)**			**Mean MINIMUM Temp (°C)**		
	2010	**10 Yr Av**	**50 Yr Av**	**2010**	**10 Yr Av**	**50 Yr Av**
Jan	4.6	6.9	5.5	-0.5	1.9	2
Feb	5.0	6.7	5.6	-1.6	1.4	1.6
Mar	8.3	8.0	7	2.5	2.2	2.3
Apr	10.4	10.6	9	3.3	3.9	3.3
May	12.3	13.0	11.4	4.7	5.7	5.5
Jun	15.7	14.8	13.7	8.7	8.1	7.8
Jul	17.1	16.7	15.2	10.0	10.2	9.7
Aug	15.6	16.5	15.4	9.2	10.3	9.9
Sep	14.0	14.8	13.6	7.8	8.9	8.6
Oct	11.7	11.8	11.2	6.3	6.4	6.9
Nov	6.8	9.0	8	1.2	3.8	4.3
Dec	4.1	7.2	6.1	-2.4	2.0	2.7
Average	10.5	11.3	10.1	4.1	5.4	5.4

Month	**RAIN (mm)**			**SUN (hrs)**		
	2010	**10 Yr Av**	**50 Yr Av**	**2010**	**10 Yr Av**	**50 Yr Av**
Jan	65.1	123.8	110.5	40.9	32.4	29.3
Feb	52.4	95.0	76.6	84.2	63.6	60.3
Mar	75.5	84.4	82.4	89.5	112.9	94.3
Apr	56.5	62.8	57.3	134.7	152.8	141.7
May	56.8	47.9	49.3	202.0	211.1	172.4
Jun	16.5	51.0	48.5	103.0	162.1	157.5
Jul	92.3	58.4	55.8	144.2	136.1	135.9
Aug	60.4	66.7	73.3	94.1	137.4	129
Sep	106.2	83.6	96.5	122.0	98.7	104.1
Oct	102.9	134.3	109.8	92.6	81.5	73.8
Nov	115.4	128.6	120.6	47.2	38.1	37.6
Dec	72.1	99.6	117.4	12.6	28.0	21.9
Totals	**872.1**	**1036.0**	**998**	**1167.0**	**1254.7**	**1157.8**

Loch of Stenness (Spence, 1914). The invertebrate fauna of the lochs is less well known and most work has focussed on the lochs of Stenness and Harray, due to the conservation interest there. In common with other areas of northern Europe, only a few native species of fish occur in Orkney, namely the brown trout (*Salmo trutta*), the European eel (*Anguilla anguilla*) and the three-spined stickleback (*Gasterosteus aculeatus*). The stoneloach (*Barbatula barbatula*) was recorded in the 1970s and the minnow (*Phoxinus phoxinus*) appeared in the late 1990s (Duncan *et al*., 1992). Both are thought to have been introduced by visiting anglers taking them to Orkney to use as livebait. Anecdotal reports exist of Atlantic salmon (*Salmo salar*) being caught in Orkney waters and the lochs of Boardhouse, Kirbister and Stenness are listed on the NASCO rivers database (NASCO, 2014). However, no evidence of successful spawning exists. Interestingly, char may also have been present in Orkney at one time. A specimen labelled *Salvelinus inframundus* (Regan, 1909) was collected from the Loch of Heldale (island of Hoy) in the 1800s and is currently held by the Natural History Museum (catalogue number 1862.9.26.2-3). Intensive sampling effort in a 1997 project failed to find any char in the loch, leading researchers to believe that the population, if it did exist, had become extinct (Kerr *et al*., 2002).

The brown trout (*Salmo trutta*) occurs widely in Orkney's lochs (Duncan *et al*., 1992). They are fished for in the major lochs of Harray, Stenness, Boardhouse, Hundland and Swanney, as well as in a number of smaller lochs such as Kirbister, Skaill and Clumly. Where lochs have suitable access to the sea, migratory sea trout occur alongside freshwater resident trout. Some troutless waters in the isles have also been stocked by the local trout fishing association, using stock from the mainland lochs (OTFA, 2014). Although there are no detailed catch data due to the open nature of the Orkney fishery, competitions are held annually on the five major mainland lochs by the Orkney Trout Fishing Association (OTFA). Results from these competitions are available dating back to the 1960s and have been summarised elsewhere, *e.g.* for Harray and Stenness competitions (ICIT, 2004). Very little is known about the utilisation of Orkney's numerous burns by trout as they are never fished due to their mainly small size. It is presumed that trout spawn in the burns inflowing the main lochs and that they represent nursery areas for juvenile trout. Some burns which drain straight to the sea are thought to be used by sea trout. Informal records of sea trout spawning in several such burns (Rossmyre, Wideford) have been kept by members of the OTFA, which operates a hatchery (G. Skea, *pers. comm.,* 20/9/2004). However, there are few data on their

productivity or the relative importance to population maintenance. The only existing quantitative data was collected by Duncan *et al*. (1992) who electrofished some of the burns serving the major mainland lochs. The highest density of trout recorded was $0.86m^{-2}$ in the Tormiston burn feeding the Loch of Harray.

This lack of data results from the fact that no formal fisheries management system exists in Orkney, as they do elsewhere in Scotland. While Orkney lies in Salmon Fishery District number 2, there has never been a Fishery Board to manage the fishing. There main reason for this is that game fishing in Orkney is largely unrestricted and free to the public. The "right" to fish for game species lies with riparian owners rather than with the Crown, as a result of Orkney's Norse heritage and the tenure of Udal law. There is no permit system and therefore no direct revenue is generated which would help to fund a Fisheries Board. While in theory, riparian owners would be within their rights to control fishing, this has never happened and in practice would be very difficult as there are multiple owners around the main lochs where the bulk of fishing activity is focused. The lack of wild salmon in Orkney is perhaps another reason why the Orkney fishery has developed in this way – had there been then things may have happened differently! As it stands, the only organisation which takes a direct interest in fisheries issues in Orkney is the OTFA, a volunteer organisation founded in 1895, which presently consists of around 500 members. It has a remit to protect and promote Orkney's trout fishing, which it does by monitoring the local environment, providing access to the main trout lochs and operating a hatchery, which it uses to stock small waters with poor or non-existent spawning burns. While it is not compulsory, local and visiting anglers are encouraged to join the OTFA. The OTFA plays an active role in trout conservation in Orkney and in the absence of a Fisheries Board or Trust is routinely consulted by the local authority on developments matters. However, it has no statutory powers to control fishing and its voluntary nature limits its ability to carry out research into the trout populations of Orkney. Nevertheless, it has helped to finance several studies on Orkney lochs and trout, such as the extensive work carried out by Stirling University's Institute of Aquaculture in the early 1990s (Duncan *et al*., 1992) and a more recent economic review, which estimated that trout fishing in Orkney was worth £1.8 million annually to the Orkney economy (SQW, 2006).

Orkney is therefore an unusual place in many respects. Its environment is not what might be expected from other regions at similar latitude. Its productive but intensively

farmed landscape sets it apart from other Scottish island groups. Its trout fishing resource and culture are clearly unique in a Scottish, if not a UK context. It is against this background that this thesis was undertaken.

2.2 Methods

Sampling of anadromous trout populations in Orkney was carried out between 2004 and 2010, inclusive. This focussed on burn habitats and was structured to provide information on the life-history stages from fry, parr and smolts through to mature resident and anadromous fish. Samples were obtained by electrofishing and trapping surveys which are described below.

2.2.1 Electrofishing

Electrofishing was used extensively throughout the fieldwork phase of this project to obtain samples of juvenile trout, smolts and mature resident trout. Electrofishing equipment comprised a WFC 911 backpack set (Electracatch International Ltd) kindly loaned to the author by the OTFA. The unit was powered by re-chargeable 24V batteries generating 0-400V smooth or pulsed DC. Electrofishing protocols generally followed that of the Scottish Fisheries Co-ordination Centre (SFCC, 2007). All surveys involved two people in the water, one of whom used the electrofishing equipment (the operator, always the author) and another, termed the assistant, worked alongside, and carried a hand net and bucket to keep the catch (Figure 2.2). The two-person team entered the water at the downstream end of the site to be fished. The operator carried out a test fishing, which allowed the assistant to set the voltage to the correct level. Once set, the team moved in an upstream direction, the operator on the left and the assistant on the right so that the anode covered the middle and both sides of the burn adequately. In narrow sections, the operator proceeded ahead and covered the full width of the burn. In all cases, the equipment was set to smooth dc as it was the opinion of the author that this worked effectively and based on observation of other surveys using pulsed dc, resulted in lower fish mortality. Generally, voltage was set at approximately 150V, unless there was a chance of encountering larger trout, in which case the voltage was lowered.

Figure 2.2: Two person electrofishing team. The operator (right) carried the electrofishing anode and a handnet. The assistant worked alongside the operator and carried a bucket and additional handnet.

Two types of electrofishing survey based on SFCC protocols were employed:

- Presence/absence (P/A) surveys were used as a rapid survey method to determine the presence of trout in a watercourse and to capture a sample for processing. The P/A survey involved a single upstream pass with no stop nets.

- Single run surveys were used to provide a semi-quantitative sample of trout from a stretch of burn that was comparable between sites and from year to year. No stop nets were used but the total time of electrofishing, typically 10 minutes, was recorded as well as the wet area of burn fished by measuring the length and width at approximately 8-10 points. Catch per unit fishing effort data (fish minute^{-1} or m^{-2}) were generated which were comparable between sites and between years. It should be noted that the sampling time was measured non-stop, *i.e.* from start to end, so included time spent removing fish from the handnets to the bucket.

In each method, fish samples were processed following the method described below and returned to the burn on completion of the survey. Habitat notes were recorded for each site, comprising observations of water depth, substrate types, water height, flow types, water temperature and conductivity, surrounding land-use and time of day.

2.2.2 Trapping

Fish traps were used in one burn to sample downstream migrating smolts in spring and the upstream migration of returning sea trout in autumn. The traps were installed in the Burn of Eyrland, conveniently located a few miles from the author's home in Stromness. The presence of a dam and fish ladder a short distance up from the sea also made this an ideal site for the installation of upstream and downstream traps (Figure 2.3). The fish ladder was located on one end of the dam and comprised a two step pool with notched walls to channel water flow. Permission to use the site was kindly provided by the owner, Mr M. Groundwater.

2.2.2.1 Downstream trap

A smolt (downstream) trap was installed each spring between 2004 and 2010, inclusive. From 2004 to 2006, the trap functioned by screening the dam and diverting fish into the fish ladder, where they were trapped as they descended into the lower pool. In 2004 & 2005, the trap consisted of a mesh-lined wooden frame (approximately 120 x 90 x 60cm) with a collar around the entrance, into which water from the upper step dropped. The 2005 version had a high sided, open, removable inner box to aid processing. In 2006, the box was replaced with a fyke net, which was attached to a wooden collar placed in the middle step of the ladder. The screens used on the dam initially used plastic mesh which was later replaced with 10mm netting with a lead footrope. Images of each of these traps are shown in Figure 2.4.

In 2007 a more effective inclined plane or "Wolf" trap was installed at the site[1] (Figure 2.5). This involved the blocking the fish ladder and channelling water over the dam and through a set of screens. The screens extended 1.2m from the lip of the dam and sloped downwards at an angle of approximately 20°. A trough made from an open pipe was positioned perpendicular to the water flow along the bottom edge of the screens, leading to closed 6" pipe which was routed into a large holding box with lid. Any smolts passing over the dam were retained by the screens and channelled via the trough into the holding box. In order to aid the passage of fish through the trap, a 1" pipe was diverted into the upper end of the trough, ensuring a continual flow of water along the trough, through the pipe and into the holding box. The trap framework was constructed of 8" x

[1] The author consulted with Russell Poole (Marine Institute, Ireland) and David Hay (Marine Scotland) over the trap design and also sought permission from SEPA prior to installation.

Figure 2.3: Dam (background) and fish ladder (foreground) at the Burn of Eyrland. The dam top was approximately 4m wide and 1m high. The fish ladder comprised three "steps" with a mean height (from water level) of approximately 300mm which fish had to negotiate in order to progress upstream.

.

2" treated timber and bolted to the bedrock on the downstream side of the 4m wide dam. The trap screens comprised 5 panels, each approximately 1.2m x 0.8m. Two screens were constructed from parallel strips of larch, approximately 12mm x 30mm in cross-section, by 120cm long. These were laid down on edge in a steel frame constructed from 50mm angle iron. A space of 10-11mm between adjacent larch strips was maintained by positioning steel nuts between each strip. These were held in place by a 4mm stainless steel threaded rod, which was threaded through the strips at four points. The wooden screen was left untreated and formed what was judged a "fish friendly" surface when wet, being flat and slippery when wet. The steel frame was painted with marine grade gloss paint. The remaining three screens were constructed from 8mm mild steel bar, welded onto a frame of 50mm steel angle iron. A gap of 10-11mm was left between adjacent bars. The screen was painted with marine grade gloss paint. The wooden screens occupied 40% of the total screen area of 4.8m^2, with an open area of just under 50%. The steel screens occupied an area of 60% with an open area of 55-60%. A low weir (50mm) was positioned on the top of the dam to direct water flow over the wooden screens at lower flows, which was overtopped in higher flows to bring the better filtering capacity of the steel screens into effect. The holding box was constructed using a fish bin, kindly donated by C. Dowie, a local workboat operator.

2004

2005

2006

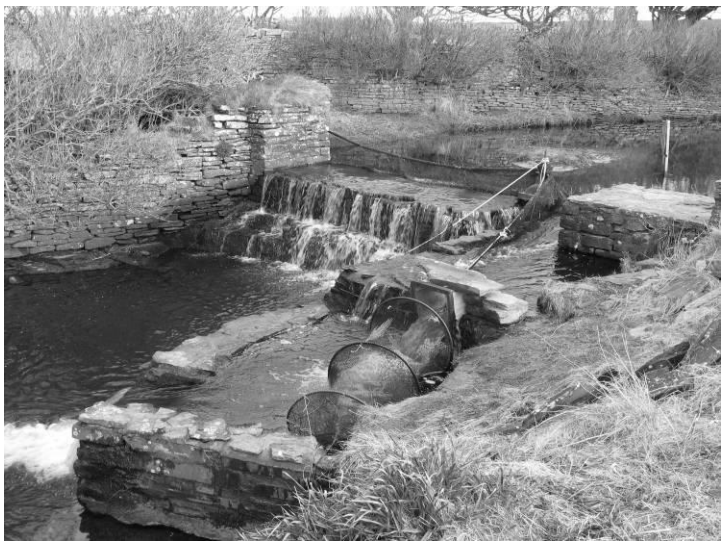


Figure 2.4: Initial fish trap designs installed at the Burn of Eyrland between 2004 & 2006. In each year the trap was installed in the fish ladder. In order to channel downstream moving fish through the fish ladder, the adjacent dam was screened off using a net or mesh.

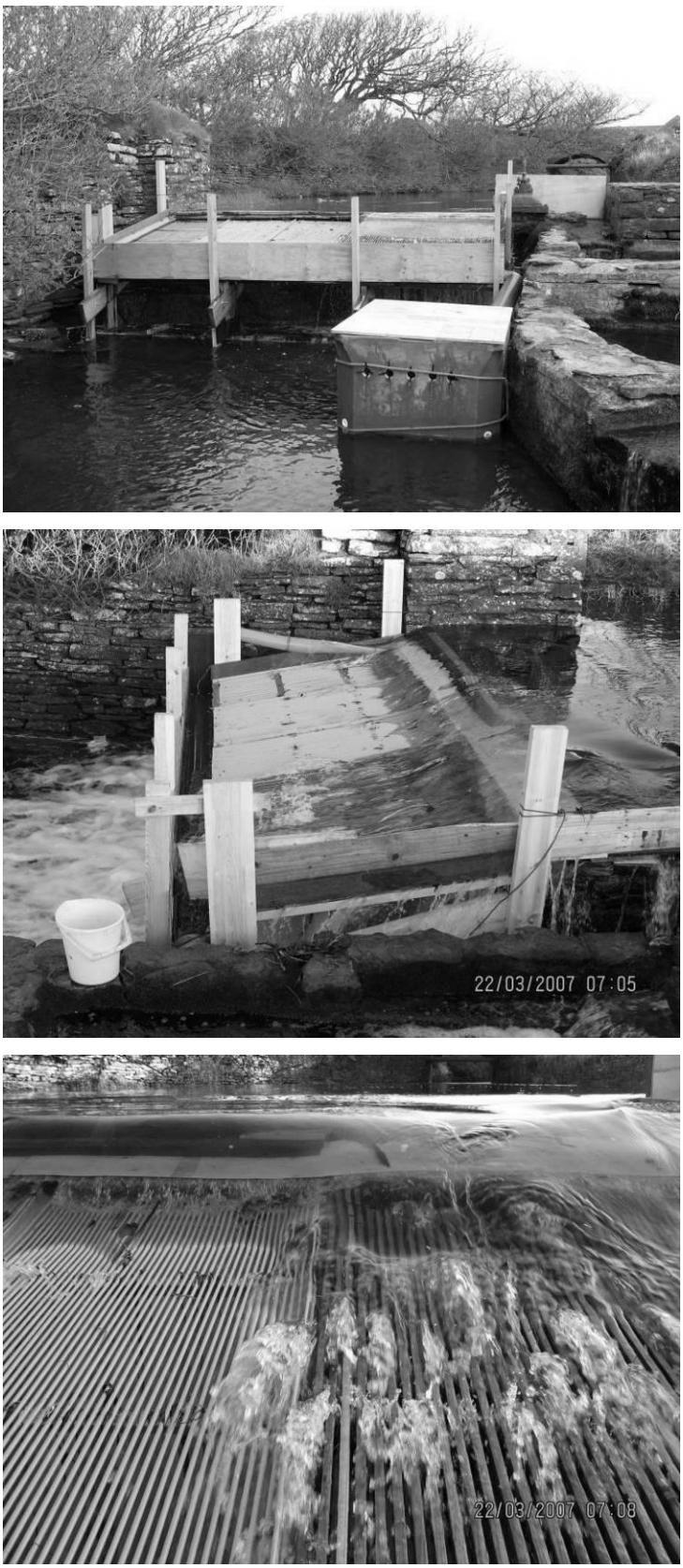


Figure 2.5: Wolf trap installed at the Eyrland burn in 2007 and operated until 2010. The trap operated by "filtering out" any downstream fish moving downstream over the dam. A combination of timber (untreated larch) and steel rod were used to construct the filter screens (bottom picture) with the former being used preferentially in low water while the latter came into effect during increased water levels. The fish ladder was screened off to channel fish over the dam.

The holding box received a continuous supply of freshwater, which drained out through mesh-lined holes cut along the top of one end. This ensured a constant exchange of water within the box. A wooden lid was fitted to prevent fish jumping out and predators from getting in. The weight of water, approximately 0.6m^3, held by the box acted as an effective anchor, but it was also tied down to prevent movement during high flows.

In each sample year, the traps were installed in mid to late March and removed in June, following the completion of the smolt migration. A water level gauge was installed in the pool upstream of the trap. The trap was checked at least once per day and more often during periods of high flow. Notes were recorded on the catch (see fish processing, below), water level and water temperature. Water conductivity was measured in some years. In later years, water temperature was recorded using TinyTag data loggers, initially set to record every six hours but later set to record hourly. On each visit, debris was removed from the trap structure to maintain a clear flow of water through screens, nets and pipes, and to prevent damage to any fish held within.

2.2.2.2 Upstream trap

An upstream trap was installed in the Burn of Eyrland in autumn 2007 and 2009 to sample sea trout returning to the burn to spawn. The trap framework was constructed from 4" x 2" timber, measured approximately 160 x 80 x 60cm and was lined with 1" galvanised steel mesh (Figure 2.6). The trap inscale, forming the entrance to the box, was initially constructed of a net "eye", taken from a fyke net. This effectively prevented fish from escaping out of the box. However, it was replaced in 2009 with a tapering channel constructed from 1" galvanised steel mesh, which was more stable under higher water flows. The trap was installed in the pool upstream of the dam, in line with the channel leading to/from the fish ladder. Fish ascending the fish ladder swam directly into the trap. The box was held in place using ropes and weights. In 2007, the trap was installed from mid-September to mid-December. In 2009 it was installed in mid August and worked through to early December. It was checked daily each morning, although additional visits were required during the main run of sea trout and during periods of high water flow. Water level, temperature and site observations were also recorded. On completion of the survey the trap was removed from the burn and stored at the nearby yard along with the smolt trap, by kind permission of D. Laidlaw, Stromness.

Figure 2.6: Upstream trap installed in the Burn of Eyrland 2007 & 2009. The trap was installed immediately upstream of the last step of the fish ladder so that any fish ascending the ladder would swim directly into the trap inscale.

2.2.3 Fish Processing

Fish samples obtained by electrofishing or trapping were processed in a broadly similar manner. A processing station was set up at the side of the sample site and comprised holding bins for storing fish prior to processing, a bucket/bin containing anaeasthetic solution to facilitate handling, a white tray to lay out the fish for measuring and recovery bins (Figure 2.7). Other equipment included a ruler/tape measure, knife for collecting scale samples, scale sample packets, digital scales, scissors, tagging equipment, thermometer and digital camera. Throughout the project, 2-phenoxyethanol was used successfully as an anaesthetic at a concentration of 0.5ml per litre, although agitation of the solution was required to ensure proper dissolution in cold water temperatures. Where possible, the author wore rubber gloves to prevent skin contact with the solution. Fish were transferred from holding bins to the anaesthetic solution and were observed until a reduction of activity and/or loss of equilibrium occurred. They were then placed onto the wetted white plastic tray for processing before being placed in a bin of freshwater to recover. When dealing with adult sea trout, one fish at a time was placed in the anaesthetic. Smaller trout (<200mm) were generally processed

Figure 2.7: Processing a sample of trout by the banks of a Hoy burn. Note from right to left the holding bin, anaesthetic bucket, white tray for measuring and finally the recovery bin. T-shirt weather was rare.

three or four at a time in the anaesthetic. Throughout the project, care was taken to maintain sufficient dissolved oxygen levels in the holding and recovery bins and the water in these was exchanged regularly during processing, especially when dealing with large numbers of fish. The anaesthetic solution was also changed periodically for the same reason. Shade for the holding and recovery bins was provided on sunny warm days. Depending on the type of survey being undertaken, processing comprised a combination of the following measurement and steps:

- length (nearest mm)
- weight (nearest 0.1g or 1g, depending on size)
- assessment of migratory stage
- scale sample
- sex determination
- tag insertion
- fin clipping
- observation of external features, *e.g.* parasites, scale damage, predator scarring

Information was recorded either onto field sheets or a white slate and later transferred to paper or electronic format. Specific processing procedures are provided in each chapter.

The assessment of development stage, particularly in relation to smolting trout was an important component of fish processing. Fish caught during springtime surveys, either in the trap or by electrofishing, were assessed visually for signs of smolting. A four-stage scale was used to categorise individual fish as follows:

B: markings typical of brown trout in freshwater, *i.e.* olive/brown with red and black spots, parr marks maybe visible, no silvering, scales not easily removed. Smolting not imminent.

1S: Brown trout markings as above but showing some signs of silvering, scales easier to remove. Smolting possible but not certain.

2S: Fish is slivering, red spots fading or gone but black spots remain, scales easily removed. Smolting imminent.

3S: Fish is almost entirely silver with few black spots, scales easily removed. Smolting imminent.

According to the above scale, fish classed as 2S or 3S were judged to be going through the smoltification process at the time of sampling and would therefore migrate to sea that spring. Smolting in fish classed as 1S or B was thought to be either unlikely or uncertain and therefore they were not included in smolt counts. A visual key to the four stages is provided in Figure 2.8. Please note that size *per se* was not used as a feature to distinguish between the four stages. For example, trout classed as "B" could also be larger than the example shown.

Maturity in resident fish sampled during autumn surveys was assessed visually. Mature males were determined by the extrusion of milt through gentle massage of the abdomen. Females were determined by a protruding vent and distended stomach.

Once processing was complete, all fish were returned to the burn. Fish caught by electrofishing were spread out over the area they had been caught, while trapped trout were released upstream or downstream depending on their direction of travel.

"B"
Freshwater resident brown trout, olive/brown in colour, black and red spots, red fin edges, parr marks sometimes visible, scales not shedding. Not smolting.

"1S"
Less distinct olive/yellow colouration and spotting with a general silvery sheen. Black and red spots still visible, parr marks may still be evident. Smolting not certain.

"2S"
Silvering but retains faint yellow/olive colouration and spotting. Scales may be looser and body is slimmer in shape. Smolting imminent.

"3S"
Smolting, body completely silver and slim, few dark spots, scales loose and maybe shedding. Smolting imminent.

Figure 2.8: Classification system used to determine the migratory status of trout sampled during springtime surveys. Smolting status in fished judged as "B" and "1S" on the scale was either unlikely or uncertain. Fished marked as "2S" or "3S" were judged as certain smolts.

2.2.4 Tagging/marking

Smolts sampled from the Eyrland burn between 2004 and 2007 were tagged using a red visual implant elastomer (VIE) tags. VIE tags (four colour packs) were obtained from Northwest Marine Technology (NMT) Ltd. The tag was prepared by mixing the desired colour with a hardening agent, in a ratio of 10:1. In practice, it was possible to mix 0.5ml of tag with 0.05ml of hardener. This was then transferred to a fine gauge syringe, which was used with an applicator to inject the tag into the fish. The preferred tag location was in the adipose tissue just posterior of the eye (Figure 2.9). Curing time varied with temperature and at room temperature the tag would set to a soft flexible plastic within a few hours. However it was possible to lengthen the working time to several days by storing the elastomer in a freezer after preparation to delay curing and transported in an insulated box with freezer packs. Tagged fish were also adipose fin-clipped. Fin clipping continued for smolts only in trap surveys from 2008 – 2010.

Figure 2.9: Fish tagging procedure. Smolts from the Eyrland burn were tagged with a red visual implant elastomer (VIE) tag manufactured by NMT Ltd. The tag was injected into the adipose tissue posterior to the right eye using a fine gauge syringe.

2.2.5 Scale reading

Scale samples were stored in small paper envelopes on which the date of sampling, fish number and other relevant details were recorded. Scale reading was done using a Zeiss Axiostar compound microscope, usually at a magnification of 40X. A digital camera mounted on the microscope was used to record scale images. Scale reading and back calculation was carried out following the method of Elliott & Chambers (1996), and was based on a simple linear relationship between fish length and scale length. The presence of B-type growth in smolt scales was defined as "growth in freshwater in the spring prior to their descent to the sea (Went, 1962). This relatively rapid growth phase is distinguished by the open growth circuli, which contrast to the closely spaced cicrculi typical of slower growth in the preceding winter growth annulus. Went (1939) described A-type (lacking B-type growth) and B-type (exhibiting B-type growth) smolts in Atlantic salmon and proposed the same nomenclature for sea trout. In this thesis, the term B-type growth was shortened to B-growth for simplicity.

2.2.6 Length nomenclature

The terms mean fork length and fork length are abbreviated to MFL and FL, respectively. However, some additional terms were used to specify size estimates in relation to the moment they applied, particularly in regard to the smolt data presented in Chapters 4 & 5. The term oMFL was used to indicate the "observed" MFL and related to the MFL in a group of fish at the time of sampling. The term cMFL was used to indicate the "corrected" MFL and related to the MFL in a group of fish at the end of the last winter annulus in freshwater. The correction was determined by back-calculation using scales from fish in the sample. In effect, this process removed any new (plus or B-growth) growth achieved in the year of sampling and standardised data so that comparisons could be made more readily especially when samples were collected at different times of the year. This process also allowed the estimation of B growth in smolts, which was effectively the difference between the cMFL and oMFL.

2.2.7 Data analysis

Data were input to Microsoft Excel for basic analysis. Statistical analyses were carried out initially using SPSS Version 14 & 16 and later using Minitab Version 17. In

general, an alpha value of 0.05 was used unless otherwise stated. Details of the specific analyses used are provided in the methods section of each chapter.

CHAPTER 3. IDENTIFICATION AND CHARACTERISATION OF ANADROMOUS BROWN TROUT POPULATIONS IN ORKNEY

3.1 Introduction

The main aim of this chapter was to determine which freshwater systems in Orkney support anadromous brown trout populations and provide a framework for more detailed investigations in later chapters. As described in Chapter 2 however, this is a significant undertaking as there are, according to Nall (1930) "a multitude of small waterways" in the islands which could potentially support trout. From a fisheries perspective, small systems tend to be overlooked probably because they are physically too small to fish in and angling attention mainly focuses on larger systems which produce larger numbers of returning adult sea trout. However, small systems are attractive choices for scientific investigation because of fieldwork practicalities and the fact that a larger portion of the overall population can be sampled. Numerous studies on sea trout populations inhabiting small streams exist in the literature (L'Abée-Lund *et al*., 1989; Titus & Mosegaard, 1989; Titus & Mosegaard, 1992; Jonsson *et al*., 2001; Limburg *et al*., 2001; Laikre *et al*., 2002; Landergren, 2004). It is interesting however that all of these studies relate to Scandinavian and, in particular, the Baltic region, where coincidentally sea trout fishing in the sea is common. Few UK examples can be cited. While the Black Brows Beck has been the subject of perhaps the most detailed long term population study ever undertaken on sea trout (Elliott, 1994), it is part of a much larger freshwater system. In his extensive work on sea trout, Nall included analyses of sea trout populations in several small systems, including two in Orkney (Nall, 1933).

In areas like Orkney, where sea trout fishing is practiced at sea rather than in freshwater, small systems (or coastal streams) collectively support what is in effect a mixed stock fishery. A similar situation exists on other areas where sea trout fishing occurs at sea, such as Shetland (Nall, 1930), the Western Isles (James, 2000) and the Baltic, *e.g.* Denmark (HELCOM, 2011). Apart from their role in supporting fisheries, the study of small systems is important for several of other reasons. Small systems are more vulnerable to environmental degradation and climate change, so the fish populations which they support are also more vulnerable (IBIS, 2012). Small systems also have a role to play in maintaining genetic diversity among sea trout populations, a trait which

has been closely linked with the economic value of salmonid fisheries (Youngson *et al*., 2003; Whelan, 2014). The need to examine small streams more closely has been acknowledged in some contemporary sea trout initiatives such as the 2004 International Sea Trout Symposium held in Cardiff (from which various papers are referenced in this thesis) and the Small Streams Workshop organised by IBIS and the Atlantic Salmon Trust (IBIS, 2012). The Moray Firth Sea Trout Project (MFSTP) is one project which has made practical advances in this area by identifying small coastal streams in the Moray Firth area which support sea trout populations (MFSTP, 2011).

In Orkney, a detailed investigation of loch-dwelling brown trout populations was undertaken in the early 1990s (Duncan *et al*., 1992). This included a limited investigation of running waters feeding the major mainland lochs. However, Orkney's coastal streams have received little recent attention. Nall (1933) studied sea trout populations inhabiting two burns on Orkney's east mainland. OTFA members have on occasion trapped sea trout in burns to collect eggs for the Association's hatchery. Detailed accounts of these efforts were kept by G. Skea (OTFA hatchery committee). Therefore, the vast majority of Orkney's coastal streams and their role in supporting anadromous trout populations remain to be properly investigated. The aims of this chapter were:

- To identify which burns in Orkney support brown trout populations and of these, which have anadromous characteristics;
- To determine if juvenile trout density and growth vary between and within populations;
- To determine the frequency, gender and growth characteristics of mature resident brown trout; and
- To determine growth and age characteristics among smolts and whether or not these vary between populations.

While these aims are relatively general, a broad approach to this initial phase of work was deemed important to set the scene and provide the context for more a more targeted approach in later chapters. It was also felt that a broad approach would be of value in a local context by providing an overall picture of sea trout occurrence in the Orkney Islands. The following pages detail the results of these investigations.

3.2 Methods

Potential trout burns in the Orkney Islands were identified using Ordnance Survey maps (OS Explorer Series, 461 - 465). After discounting burns which flowed over cliffs into the sea and drainage ditches, a total of 82 burns were selected for survey. The candidate burns were located on the Orkney mainland, the linked south isles of South Ronaldsay and Burray and the islands of Hoy and Rousay. Burns on the outer north isles of Westray, Papa Westray, Sanday, Stronsay, Eday, Shapinsay and North Ronaldsay were not surveyed although few are thought to exist there.

3.2.1 Sampling

Sampling in this phase of work was carried out exclusively by electrofishing. Presence/absence (P/A), single run (semi-quantitative) and three run (quantitative) surveys were used to collect samples. P/A surveys were used as relatively rapid technique in the initial phase of work to determine which burns supported trout and were carried out at various times of the year from spring, through summer and into autumn. Therefore, depending on the season, P/A surveys provided samples of smolts, mature resident trout and returning sea trout, as well as resident immature juvenile fish. Survey sites were generally located in the downstream reaches of each burn, close to the tidal limit, so that smolts might be sampled if present. This also allowed an inspection of the burn mouth and access conditions to the sea. In some cases, additional survey sites were selected further upstream, particularly if the initial downstream survey had failed to find any trout.

In order to provide more robust data for the comparison of density and growth trends, single run (semi-quantitative) surveys were employed on a smaller number of streams where the presence of anadromous trout populations had been established from the P/A surveys. Single run surveys were carried out at four burns in 2005 to provide measures of trout density and growth. Multiple sample sites were spread along the length of each burn from the tidal limit to the upper reaches. Sampling effort at each site was recorded as the total fishing time (10 minutes) and the wet area fished. Results were used to make intra- and inter-population comparison of these characteristics. Single run surveys were carried out in late autumn so that *inter alia* the first summer's growth in 0+ trout could be examined. This timing also allowed any mature trout (freshwater resident and sea trout) in each population to be sampled. Results from single run

surveys were compared to the Fisheries Classification Scheme developed for the classification for salmonid populations in streams of less than 4m width (Godfrey, 2005).

Full descriptions of electrofishing methodologies are provided in Chapter 2. The location and other physical details for presence/absence and semi-quantitative survey sites are provided in Appendices A and B. Maps showing the location of semi-quantitative sites are provided in Appendix C.

3.2.2 Processing

All fish samples were processed according to the procedure described in Chapter 2.

3.2.3 Data analysis

Data analysis was carried out using SPSS, versions 14 and 16. In general, one-way ANOVA was used to compare fork length data between sites and burns. In comparisons involving more than 2 groups, a Fishers LSD post hoc test was used to determine which groups were significantly different from each other. Relationships between two variables was tested using regression. A p-value of 0.05 was used unless stated otherwise.

3.3 Results

Survey work was carried out between 2004 and 2009 inclusive. Results from these surveys are detailed below.

3.3.1 Occurrence of anadromous populations

Presence/absence electrofishing surveys were carried out in 82 burns at varying times of the year between 2004 and 2009. Brown trout, *Salmo trutta,* were found in 36 burns and yielded a total sample of 1091 fishes comprising parr, smolts, mature resident trout and mature sea trout. Most trout burns were found on the Orkney mainland (26), with smaller numbers in Hoy (7) and Rousay (3). The locations of burns where trout were found are shown in Figure 3.1 and detailed in Appendix A. Raw survey data for each burn where trout were found are provided electronically in Appendix D.

Evidence of anadromy was found in 23 burns (hereafter referred to as sea trout burns): smolts (N = 220) were found in 21 during spring surveys, while returning sea trout were found in an additional two during autumn surveys. The majority of sea trout burns were located on the mainland (17) with the remainder being found on Hoy (4) and Rousay (2). In the remaining 13 burns, resident trout only were found in 10, while in three, the entire sample comprised a single finnock. In the absence of resident trout, those three burns were <u>not</u> classified as supporting anadromous populations. Forty-six burns yielded no trout, even after random repeat sampling although some did support other species, namely the three-spined stickleback (*Gasterosteus aculeatus*) and/or the European eel (*Anguilla anguilla*).

Scale reading revealed that the total sample (excluding sea trout & finnock) comprised trout of all ages up to five years, although most were aged between one and three. The back calculated MFL of one, two and three year old trout sampled from 29 burns is provided in Table 3.1. Seven burns were discounted from this analysis as the sample size from each was either too small (<5) or where only 0+ trout were found. Between populations, the cMFL to the end of the last winter annulus in one year old trout varied between 70.1mm – 105.1mm, two year olds between 114.9mm - 202.2mm and three year olds between 143.2mm – 297.0mm. An "Orkney average" was produced by averaging the cMFL of each age cohort from each population and is shown in Figure 3.2.

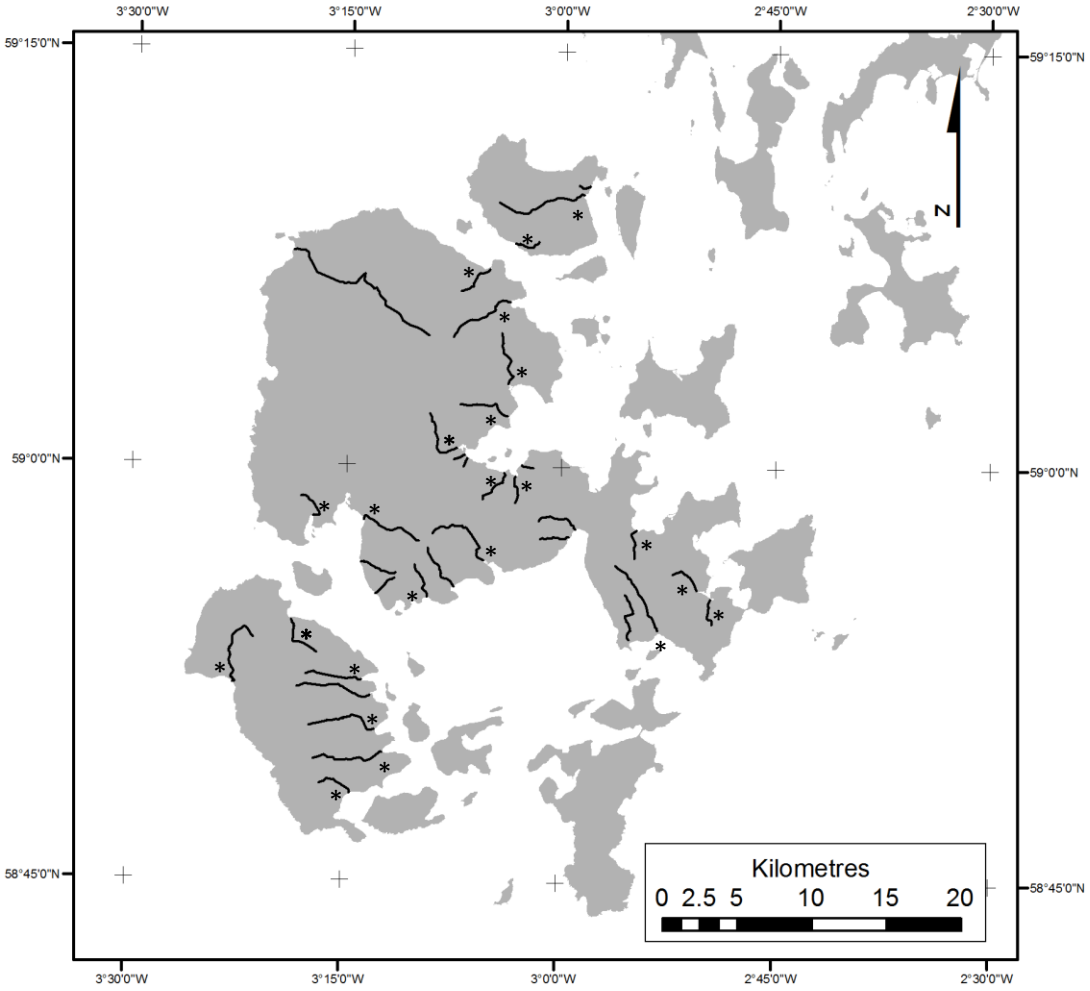


Figure 3.1: Map showing the location of burns where brown trout (Salmo trutta) were found by electrofishing, 2004 – 2009. In burns marked with a "", evidence of anadromous activity was found.*

Table 3.1: cMFL (mm) of one, two and three year-old trout in each population of trout sampled from Orkney burns, 2004-2009. Length at the end of the last winter annulus was estimated by back-calculation. "nd" = no data, i.e. no fish of that age were found.

Burn	N	1yr olds cMFL±se (N) (mm)	2yr olds cMFL±se (N) (mm)	3 yr olds cMFL±se (N) (mm)
1. Binscarth	56	99.6 ± 3.3 (36)	146.1 ± 7.0 (14)	185 ± 20.2 (3)
2. Boardhouse	15	nd	202.2 ± 5.7 (11)	297.0 (1)
3. Bu	93	100.2 ±4.5 (58)	146.8 ±7.5 (12)	nd
4. Burness	49	96.2 ±2.5 (41)	183.1 ± 17.5 (3)	nd
5. Caldale	20	101.2 ±3.3 (5)	159.3 ± 13.5 (4)	219.7 (1)
6. Desso	34	88.1 ±3.5 (21)	166.9 ± 5.5 (10)	239.0 (1)
7. Eyrland	103	97.0 ±2.3 (46)	150.7 ± 3.8 (54)	189.2 ± 14.9 (3)
8. Graemeshall	39	90.9 ±3.0 (39)	nd	nd
9. Heldale	2	89.0 (1)	nd	171.9 (1)
10. Hullion	29	76.5 ±2.9 (17)	142.5 ± 5.5 (5)	164.1 ± 20.2 (2)
11. Isbister	51	99.1 ±2.0 (48)	151.3 ± 23 (3)	nd
12. Kirbister	48	85.9 ±2.7 (30)	158.3 ± 4.4 (11)	Nd
13. Lyrawa	8	70.1 ±1.5 (4)	117.5 (1)	143.1 ± 7.8 (3)
14. Maitland	10	80.4 ±3.9 (7)	114.9 ± 4.6 (2)	242.0 (1)
15. Mill	25	99.5 ±2.6 (12)	140.4 ± 4.6 (12)	nd
16. Oklester	22	105.1 ±2.8 (21)	166.5 (1)	nd
17. Ore	44	79.2 ±2.2 (27)	134.8 ± 7.3 (7)	172.6 ±15.2 (6)
18. Pegal	9	nd	119.2 (1)	164.4 ±9.4 (2)
19. Rackwick	40	85.7 ±5.5 (8)	114.9 (1)	169.0 (1)
20. Rennibister (East)	2	95.2 ±4.0 (2)	nd	nd
21. Rennibister (West)	20	80.1 ±2.1 (20)	nd	nd
22. Rossmyre	61	87.0 ±2.1 (48)	159.6 ± 5.5 (9)	nd
23. Sebay	34	88.0 ±3.3 (15)	140.5 ± 4.4 (12)	nd
24. Sourin	45	89.6 ±3.8 (17)	148.6 ± 5.1 (12)	195.0 (1)
25. Stromness Mill Burn	7	111.0 (1)	179.1 ± 13.4 (5)	nd
26. Swanbister	19	102.1 ±2.8 (13)	155.8 ± 10.2 (5)	208.0 ±16.0, (2)
27. Wideford	22	93.7 ±3.3 (11)	173.0 ± 13.4 (2)	223.0 (1)
28. Whaness	41	73.0 ±2.1 (18)	118.1 ± 3.7 (11)	143.6 ±7.4 (3)
29. Woodwick	33	93.9 ±2.6 (17)	160.4 ± 7.3 (7)	nd

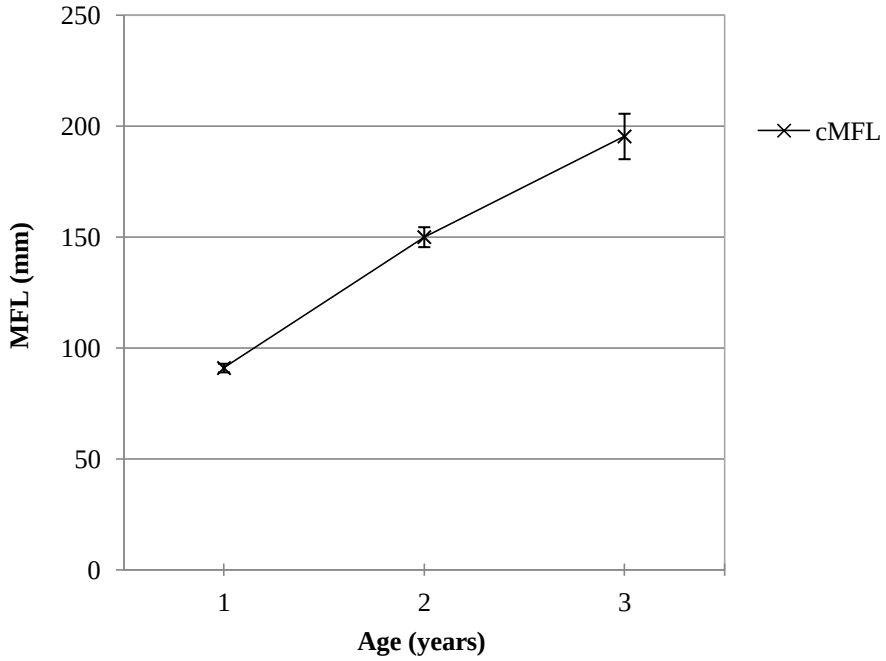


Figure 3.2: Average cMFL ±se (mean of each population average) for one, two and three year old trout sampled by electrofishing from 29 burns in the Orkney Islands between 2004 and 2009. Length corrected by back calculation to the end of the last winter annulus for each age cohort.

3.3.2 Single run (semi-quantitative) surveys 2005

Single run (semi-quantitative) electrofishing surveys were carried out the burns of Eyrland, Bu, Rossmyre and Isbister, each located on the west mainland of Orkney. All burns were sampled within a four week period. A summary of results is provided in Table 3.2 while raw data are provided in Appendix E. Length – frequency graphs for the sample of trout from each burn are shown in Figure 3.3. The sample from each burn consisted mainly of resident trout (immature and mature), although small numbers of returning sea trout were also caught.

Eyrland burn

Nine sites were surveyed between the 6th and 9th October 2005. Trout were distributed throughout the system although fewer were found at the furthest upstream sites. Catch rate varied from 0.4 to 2.7 trout per minute. The sample comprised trout aged 0+, 1+ and 2+. The mean density (100m^{-2}) of 0+ and 1++ trout was 13.5 and 8.0, respectively. Trout aged 0+ made up 59% of the entire sample. The MFL of 0+ trout varied between sites from 69.5mm to 92.8mm. In total, 42 mature resident trout were recorded, 40 of

which were male. Most of the male trout were found in the middle to upper reaches of the main branch. A total of six sea trout were found at sites IR-T2, IR-T3 and IR-T5. These included finnock and mature trout of age 2.1+. All were female and two had been tagged as smolts leaving the burn in spring 2004.

Bu burn

Six sites were surveyed on the 4th November 2005. Trout were numerous at all sites apart from T6, upstream of a road culvert, where only a single fish was found. Catch rate varied between 3.5 and 4.8 trout min^{-1}, the highest of the four burns. The sample comprised trout aged 0+ and 1+. The mean density ($100m^{-2}$) of 0+ and 1++ trout at the five lower sites was 56.4 and 4.5, respectively. Trout aged 0+ predominated, making up 92% of the entire sample. The MFL of 0+ trout at each site varied from 79.0mm to 92.4mm. A total of 9 mature resident trout were found, all of which were male. One mature female sea trout was found at site BU-T2.

Isbister burn

Nine sites were surveyed between the 2nd and 3rd November 2005. Trout were found at all sites. Catch rate varied from 0.6 – 3.7 trout min^{-1}. The sample comprised trout aged 0+, 1+ and 2+. The mean density ($100m^{-2}$) of 0+ and 1++ trout was 13.7 and 6.2, respectively. Trout aged 0+ made up 60% of the entire sample. The MFL of 0+ trout varied from 71.6 – 103.4mm. Of the 18 mature resident trout found, 16 were male. They were found throughout the catchment apart from sites IS-T1 and IS-T3. Two mature sea trout were recorded at the downstream sites: one finnock at IS-T1 and a mature male sea trout (age 2.1+) at IS-T2.

Rossmyre burn

Seven sites were surveyed on the 19th October 2005. Trout were found at all sites. Catch rate varied from 1.3 – 4.4 trout min^{-1}. The sample comprised trout aged 0+, 1+ and 2+. The mean density ($100m^{-2}$) of 0+ and 1++ trout was 37.6 and 10.3, respectively. Trout aged 0+ made up 74% of the entire sample. The MFL of 0+ trout varied 72.7 – 86.6mm. A total of 12 mature residents were found, all male. Four sea trout were found, a finnock at RM-T1 and another finnock and two mature male sea trout (both 1.1+) at RM-T2.

Table 3.2: Results of semi-quantitative (single run, timed) electrofishing surveys carried out the burns of Eyrland (6th/7th/9th October), Bu (4th November), Isbister (2nd/3rd November) and Rossmyre (19th October) in autumn 2005. Results are expressed in terms of catch per unit effort (trout per minute and trout per 100m^2) and are also broken down by age. Numbers of mature resident males and females are shown as well as any sea trout. Furthest downstream sites in each burn are indicated by a "".*

	Site	Area (m^2)	No. of trout	No. trout (min^{-1})	No. 0+ (%)	MFL 0+ (mm, ±se)	Density 0+ ($100m^{-2}$)	Density 1++ ($100m^{-2}$)	Mature residents ♂	Mature residents ♀	Sea trout ♂	Sea trout ♀	Sea trout Imm.
Eyrland	IR-T1*	99.4	17	1.7	12 (71%)	90.7 ± 3.1	12.1	5.0	2	-	-	-	-
	IR-T2	68.0	25	2.5	16 (64%)	91.8 ± 1.5	23.5	13.2	4	-		1	-
	IR-T3	131.5	19	1.9	8 (42%)	87.0 ± 3.4	6.1	8.4	4	1	-	3	1
	IR-T4	124.8	26	2.6	16 (62%)	92.8 ± 2.2	12.8	8.0	5	1	-	-	-
	IR-T5	111.7	26	2.6	18 (69%)	86.6 ± 1.3	16.1	7.2	11	-	-	1	-
	IR-T6	86.3	27	2.7	17 (63%)	82.8 ± 1.4	19.7	11.6	7	-	-	-	-
	IR-T7	81.0	7	0.7	0 (0%)	-	0.0	8.6	6	-	-	-	-
	IR-T8	51.2	4	0.4	4 (100%)	69.5 ± 6.4	7.8	0.0	-	-	-	-	-
	IR-T9	38.5	13	1.3	10 (69%)	69.6 ± 2.1	23.4	10.4	1	-	-	-	-
	Total/Average for all sites	792.4	172	2.0	101 (59%)	83.9 ± 1.0	Av = 13.5	Av = 8.0	40	2	0	5	1

	Site	Area (m^2)	No. of trout	No. trout (min^{-1})	No. 0+ (%)	MFL 0+ (mm, ±se)	Density 0+ ($100m^{-2}$)	Density 1++ ($100m^{-2}$)	Mature residents ♂	Mature residents ♀	Sea trout ♂	Sea trout ♀	Sea trout Imm.
Bu	BU-T1*	111.8	37	3.7	34 (87%)	92.4 ± 1.5	28.6	4.5	2	-	-	-	-
	BU-T2	64.1	48	4.8	42 (88%)	85.4 ± 1.9	65.5	9.4	4	-	-	1	-
	BU-T3	53.8	35	3.5	35 (100%)	89.1 ± 1.8	65.1	0.0	-	-	-	-	-
	BU-T4	56.6	35	3.5	34 (97%)	91.7 ± 2.0	60.1	1.8	1	-	-	-	-
	BU-T5	30.2	39	3.9	36 (92%)	79.0 ± 2.0	119.2	9.9	2	-	-	-	-
	BU-T6	65.0	1	0.1	0 (0%)	-	0.0	1.5	-	-	-	-	-
	Total/Average for all sites	381.5	196	3.3	181 (92%)	87.3 ± 0.9	Av = 56.4	Av = 4.5	7	0	0	1	0

Table 3.2: continued.

Isbister

Site	Area (m^2)	No. of trout	No. trout (min^{-1})	No. 0+ (%)	MFL 0+ (mm, ±se)	Density 0+ ($100m^{-2}$)	Density 1++ ($100m^{-2}$)	Mature residents ♂	Mature residents ♀	Sea trout ♂	Sea trout ♀	Sea trout Imm.
IS-T1*	118.1	6	0.6	5 (83%)	103.4 ± 2.3	4.2	0.8	-	-	1	-	-
IS-T2	182.3	24	2.4	12 (50%)	102.9 ± 1.6	6.6	6.6	3	1	1	-	-
IS-T3	128	10	1.0	3 (30%)	94.3 ± 4.8	2.3	5.5	-	1	-	-	-
IS-T4	85.6	19	1.9	9 (47%)	96.4 ± 1.8	10.5	11.7	2	-	-	-	-
IS-T5	279.3	6	0.6	2 (33%)	93.5 ± 0.5	0.7	1.4	1	-	-	-	-
IS-T6	117	17	1.7	9 (53%)	99.0 ± 3.9	7.7	6.8	3	-	-	-	-
IS-T7	43.4	37	3.7	32 (86%)	71.6 ± 2.2	73.7	11.5	2	-	-	-	-
IS-T8	81.3	10	1.0	7 (70%)	85.3 ± 5.1	8.6	3.7	2	-	-	-	-
IS-T9	78.2	13	1.3	7 (54%)	93.0 ± 4.4	9.0	7.7	3	-	-	-	-
Total/Average for all sites	1113.2	143	1.6	86 (60%)	87.5 ±1.8	Av = 13.7	Av = 6.2	16	2	2	0	0

Rossmyre

Site	Area (m^2)	No. of trout	Overall catch (min^{-1})	No. 0+ (%)	MFL 0+ (mm, ±se)	Density 0+ ($100m^{-2}$)	Density 1++ ($100m^{-2}$)	Mature residents ♂	Mature residents ♀	Sea trout ♂	Sea trout ♀	Sea trout Imm.
RM-T1*	70	22	2.2	16 (76%)	85.7 ± 2.8	22.9	8.6	1	-	-	-	1
RM -T2	67.7	31	3.1	7 (23%)	86.0 ± 5.7	10.3	35.5	8	-	2	-	1
RM -T3	73.3	44	4.4	37 (84%)	85.0 ± 1.6	50.5	9.5	1	-	-	-	-
RM -T4	61.9	13	1.3	9 (69%)	86.6 ± 3.3	14.5	6.5	1	-	-	-	-
RM -T5	43.7	21	2.1	20 (95%)	81.7 ± 2.0	45.8	2.3	1	-	-	-	-
RM -T6	24.9	26	2.6	24 (92%)	79.4 ± 2.2	96.4	8.0	-	-	-	-	-
RM -T7	61.3	15	1.5	14 (93%)	72.7 ± 2.4	22.8	1.6	-	-	-		-
Total/Average for all sites	402.8	172	2.5	127 (74%)	82.4 ± 1.0	Av = 37.6	Av = 10.3	12	0	2	0	2

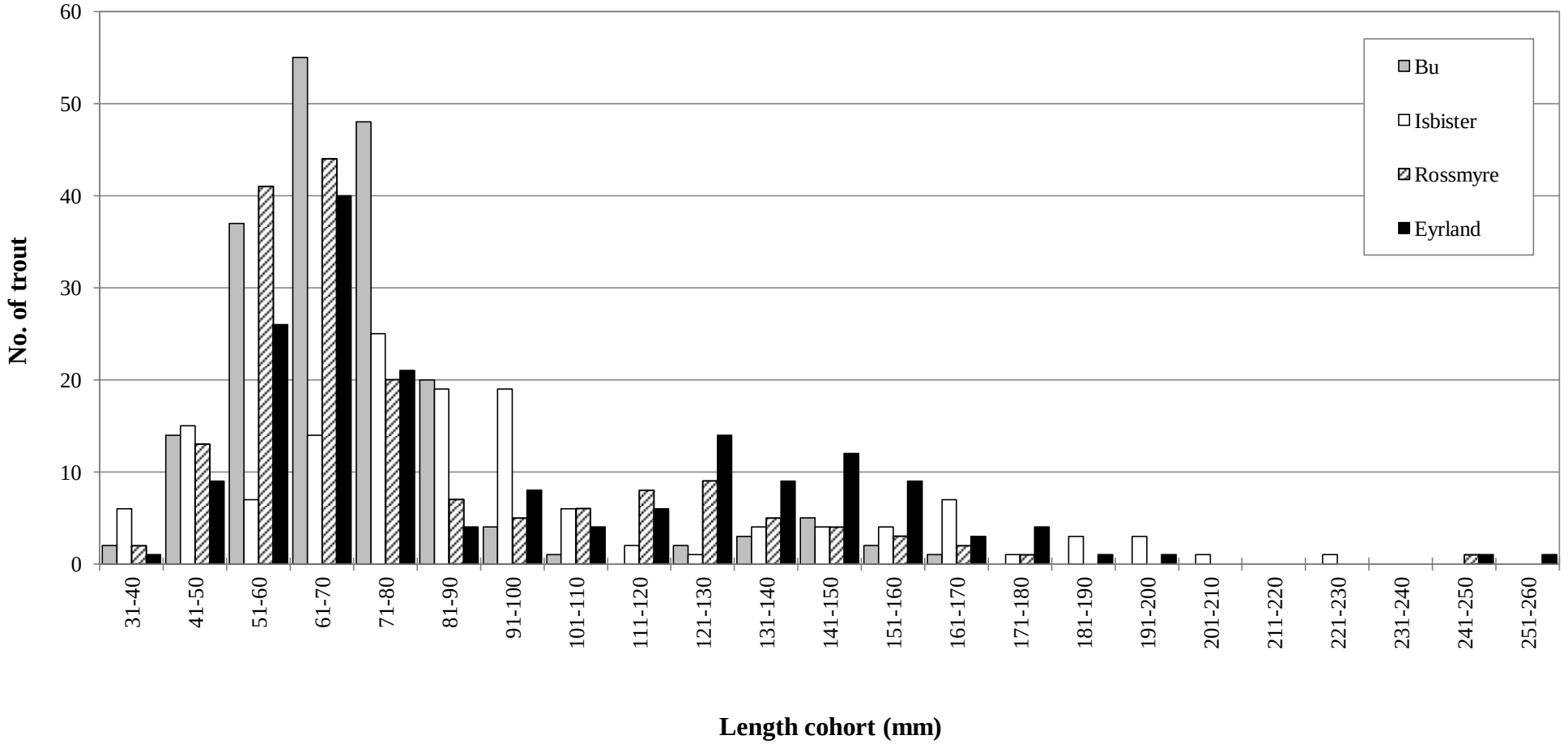


Figure 3.3: Length frequency data for trout sampled from the burns of Bu, Isbister, Rossmyre and Eyrland, October & November 2005 by semi-quantitative (timed) electrofishing survey (excludes sea trout).

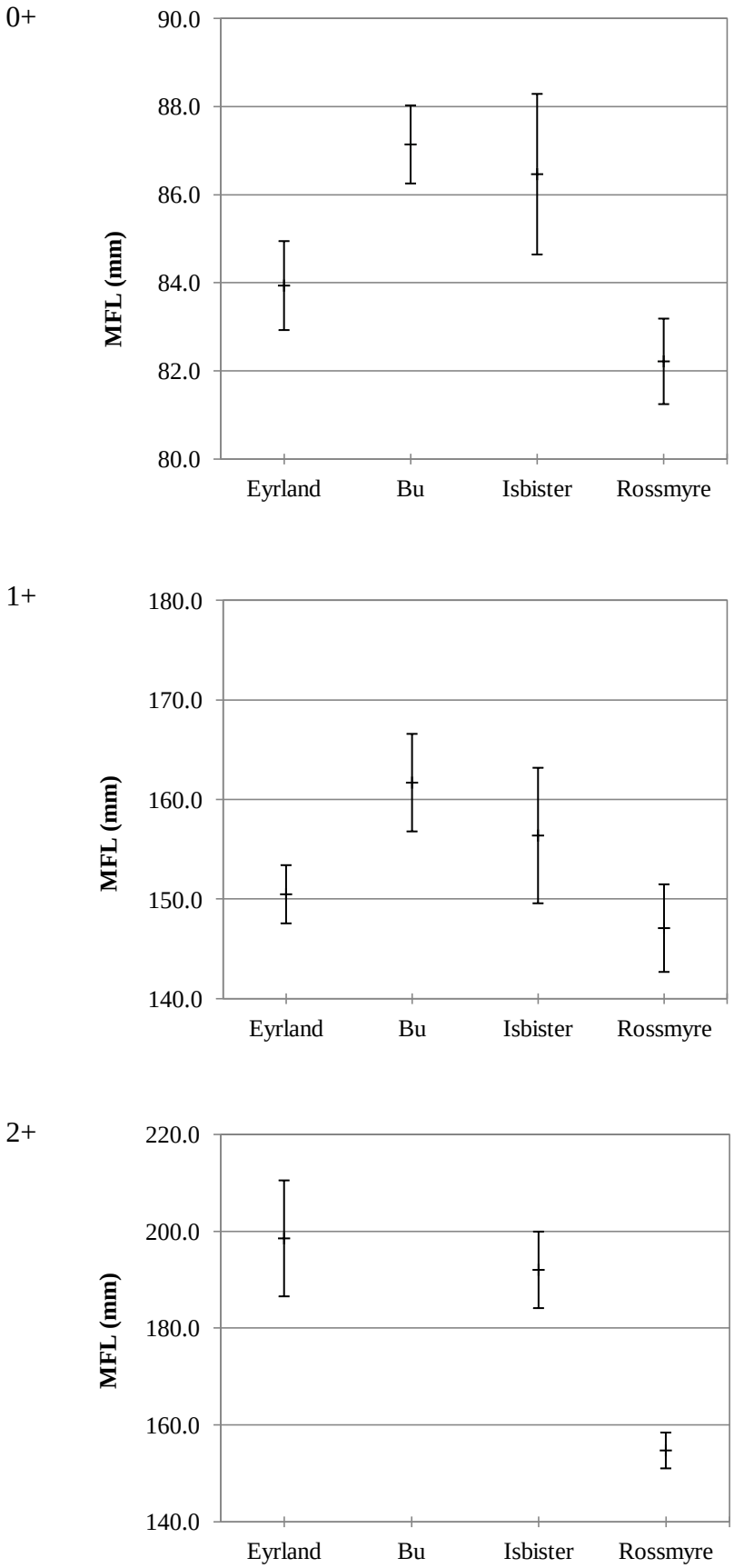


Figure 3.4: MFL ±se for 0+, 1+ and 2+ trout sampled from the burns of Bu, Eyrland, Isbister and Bu, sampled during semi-quantitative (single-run) electrofishing surveys carried out in autumn 2005.

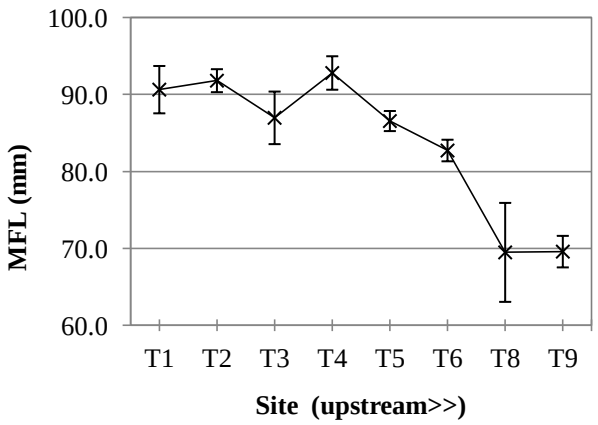
MFL for each age cohort in each burn are shown in Figure 3.4. Trout aged 0+ were largest in the Bu followed by Isbister, Eyrland and Rossmyre. One way ANOVA showed a significant difference in MFL between 0+ trout from each population ($F(3, 457) = 6.199$, $p < 0.001$). Post hoc comparisons using the Fisher LSD test showed that 0+ trout from the Bu and Isbister burns were similar in size but both were significantly larger than 0+ trout from the Rossmyre burn. Moreover, 0+ trout from the Bu were significantly larger than those from the Eyrland burn. In the Eyrland and Rossmyre burns, 0+ trout were similar in size. There was no significant difference in the MFL of 1+ trout ($F(3, 98) = 1.5337$, $p = 0.211$) or 2+ ($F(3, 17) = 2.46449$, $p = 0.114$) between the four populations. It should be noted however that in each population the sample sizes for trout aged 1+ and 2+ were much smaller than for 0+ trout, particularly in the latter case.

Within each population, growth varied between sample sites, particularly among 0+ trout. One way ANOVA showed that MFL of 0+ trout varied significantly between sites in each burn:

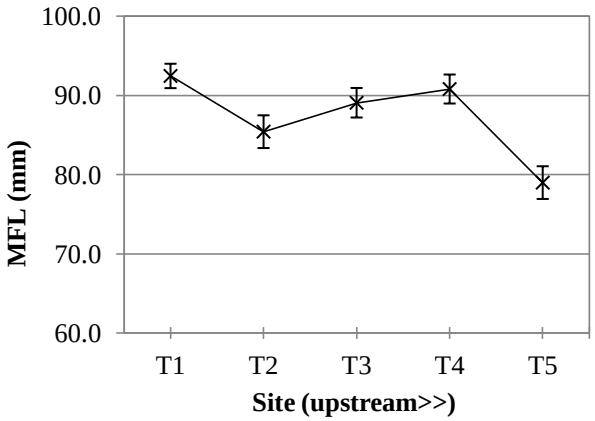
Eyrland: $F(8,92) = 9.975$, $p < 0.001$
Bu: $F(4,175) = 8.344639$, $p < 0.001$
Isbister: $F(8,77) = 16.595$, $p = 0.001$
Rossmyre: $F(6,120) = 3.306$, $p < 0.05$

The general trend in each population was for MFL to decrease with upstream distance as illustrated in Figure 3.5. Post hoc comparisons using the Fisher LSD test showed that these differences were significant and in each of the four populations, MFL at the furthest upstream sampling sites was significantly smaller than those further downstream (Table 3.3). Similar analysis was not carried out with 1+ and 2+ trout as the sample sizes were much smaller.

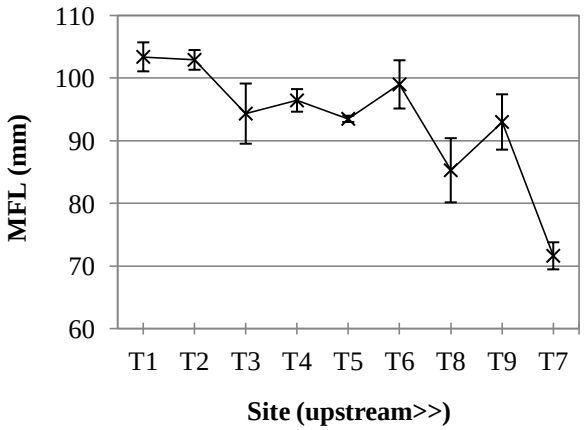
Eyrland



Bu



Isbister



Rossmyre

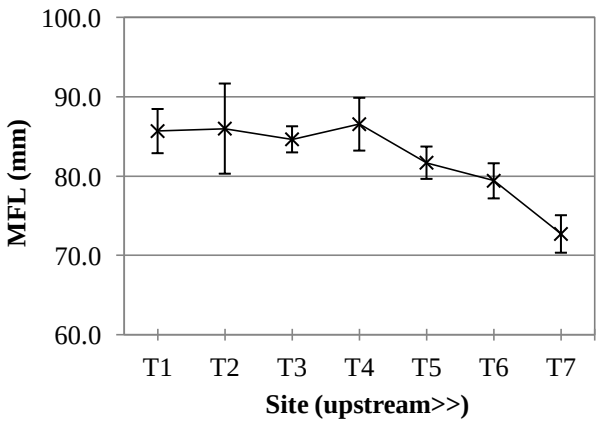


Figure 3.5: Relationship between MFL (±se) of 0+ trout and site (increasing distance upstream) in the burns of Eyrland, Bu, Isbister & Rossmyre, in autumn 2005.

Table 3.3: Post hoc (Fishers LSD) comparisons of MFL between 0+ trout at different sample sites in the burns of Eyrland, Bu, Isbister & Rossmyre, sampled in autumn 2005. MFL that do not share a letter are significantly different. Further upstream site in each burn is indicated with an "".*

Burn	Site	N	MFL (mm)	Grouping			
Eyrland	1	12	90.7	A			
	2	16	89.6	A			
	4	16	89.3	A			
	3	8	87.0	A	B		
	5	18	83.6		B	C	
	6	17	79.7			C	
	9*	10	69.6				D
	8	4	69.5				D
Bu	1	34	92.4	A			
	4	33	90.8	A			
	3	35	89.1	A	B		
	2	42	85.4		B		
	5*	36	79.0			C	
Isbister	1	5	103.4	A	B		
	2	12	102.9	A			
	6	9	99.0	A	B		
	4	9	96.4	A	B		
	8	7	96.0	A	B		
	3	3	94.3	A	B		
	5	2	93.5	A	B		
	9	7	93.0		B		
	7*	32	71.6			C	
Rossmyre	4	9	86.6	A			
	2	7	86.0	A			
	1	16	85.7	A			
	3	37	84.6	A			
	5	20	81.7	A			
	6	24	79.4	A	B		
	7*	14	72.7		B		

Table 3.4: Comparison of MFL between mature resident trout and same aged immature residents in the burns of Eyrland, Bu, Isbister & Rossmyre, sampled in autumn 2005. "nd" = no data either because there were no fishes in the group of that age could not be determined confidently from scale analysis.

	1+ MFL ±se (N) (mm)		2+ MFL ± se (N) (mm)	
Burn	Immature	Mature	Immature	Mature
Eyrland	148.4 ±3.6 (27)	152.6 ±4.7 (26)	nd	189.7 ±12.0 (7)
Bu	164.5 ±10.4 (6)	159.6 ±4.2 (4.2)	nd	nd
Isbister	136.6 ±6.8 (7)	170.2 ±8.2 (10)	194.1 ±8.5 (9)	173.0 ± nd (1)
Rossmyre	148.6 ±4.9 (14)	141.5 ±2.0 (4)	154.7 ±3.7 (3)	nd

Of the 79 mature parr found in total, only four were female and 75 (95%) were male. Of the 56 males which were scale sampled, 47 were aged 1+ with nine aged 2+. MFL data for mature resident trout is shown in Table 3.4. In the Isbister system, mature trout aged 1+ were significantly longer than immature trout of the same age (one way ANOVA, $F(1,15) = 8.793$, $p < 0.05$). The same comparison in 1+ trout from the other burns yielded no significant differences (Eyrland, $F(1,51) = 0.513$, $p = 0.477$; Bu, $F(1,12) = 0.231$, $p = 0.639$; Rossmyre, $F(1,16) = 0.419$, $p = 0.526$). There were insufficient data on 2+ trout to carry out the same analysis for individual burns.

3.3.3 Smolt characteristics

During the presence/absence survey phase, a total of 220 smolts were sampled from 21 burns over the period 2004 – 2009 (Table 3.5). Raw data are contained in Appendix D. Mean size at sampling (oMFL) varied from 123.0mm in Wideford to 173.6mm in Eyrland and the mean length of all individuals was 151.7mm (± 1.4mm). After correcting for any B-growth, the mean smolt size at the end of winter (cMFL) was 131.7mm (± 1.9mm). Scale reading also indicated that S2 smolts were most numerous (59%) followed by S1s (33%) then S3s (8%), with a single S4 smolt captured from the Lyrawa Burn in Hoy. MSA varied from 1.0 years in Wideford and Graemeshall to 3.3 years in Lyrawa. Overall MSA was 1.9 yrs (± 0.1yrs).

Back-calculated lengths of S1, S2 and S3 smolts (B-growth removed) are shown in Figure 3.6. The youngest smolts (S1s) exhibited the fastest freshwater growth rate, which decreased with age in S2 and S3 smolts. Comparisons of size at different ages (yrs) were made using one way ANOVA. This showed that after one year's growth, trout which smolted at age one were significantly larger than those which smolted at two years old ($F(1,173) = 193.993$, $p < 0.001$), which in turn were significantly larger than those which smolted at age three ($F(1,126) = 9.289$, $p < 0.005$). After two years growth trout which smolted at age two were significantly larger than those which smolted at three years old ($F(1,126) = 32.914$, $p < 0.001$). The finally comparison concerned the size of S1 smolts and S3 smolts at age two. While the S3 smolts were slightly larger at age two in comparison to S1 smolts, the difference was not significant ($F(1,75) = 1.257$, $p > 0.05$).

Table 3.5: Smolt length and age characteristics in 21 Orkney burns, sampled by single-run electrofishing, 2004 – 2009. MFL is presented at time of sampling (oMFL) and at the end of the last winter annulus (cMFL).

Burn	N_{smolts}	oMFL ± se (mm)	cMFL ± se (mm)	MSA ± se (yrs)
1. Binscarth	24	153.0 ± 4.7	132.9 ± 5.1	1.6 ± 0.1
2. Bu	39	140.6 ± 3.2	121.7 ± 6.7	1.6 ± 0.1
3. Burness	6	143.5 ± 4.3	125.1 ± 11.0	1.3 ± 0.3
4. Desso	4	157.0 ± 4.7	143.6 ± 6.5	1.8 ± 0.3
5. Eyrland	29	173.6 ± 3.8	150.1 ± 4.5	2.0 ± 0.1
6. Graemeshall	13	137.1 ± 3.2	101.4 ± 4.0	1.0 ± 0.0
7. Hullion	5	153.6 ± 5.0	142.5 ± 5.5	2.0 ± 0.0
8. Isbister	9	149.3 ± 2.9	121.4 ± 5.1	1.7 ± 0.2
9. Kirbister	4	163.0 ± 12.5	143.2 ± 12.4	1.8 ± 0.3
10. Lyrawa	4	164.8 ± 6.4	141.2 ± 3.4	3.3 ± 0.3
11. Mill	9	148.2 ± 2.4	135.9 ± 4.3	2.0 ± 0.0
12. Oklester	13	139.4 ± 4.4	115.8 ± 5.2	1.1 ± 0.1
13. Ore	8	161.5 ± 7.8	146.6 ± 8.8	2.5 ± 0.2
14. Rackwick	1	169.0 ± nd	169.0 ± nd	3.0 ± nd
15. Rossmyre	9	154.4 ± 6.2	144.5 ± 10.8	1.9 ± 0.1
16. Sebay	18	149.8 ± 4.3	121.6 ± 6.9	1.6 ± 0.1
17. Sourin	8	162.0 ± 4.6	152.7 ± 4.9	2.0 ± 0.0
18. Stromness Mill burn	3	161.6 ± 5.5	148.7 ± 4.4	2.0 ± 0.0
19. Whaness	11	144.2 ± 3.8	134.0 ± 4.8	2.5 ± 0.2
20. Wideford	2	123.0 ± 1.0	101.7 ± 7.1	1.0 ± 0.0
21. Woodwick	1	169.0 ± nd	169.0 ± nd	2.0 ± nd
TOTAL	**220**	**151.7 ± 1.4**	**131.7 ± 1.9**	**1.9 ± 0.1**

Mean first year growth was compared to the mean smolt age and mean smolt length in each of the 21 populations where smolts were sampled (Figure 3.7). Regression analysis indicated a significant inverse relationship between mean first year growth and mean smolt age ($df = 19$, $R = 0.558$, $p < 0.05$) across the sample populations. However, there was no significant relationship between the first year's growth increment and smolt size ($df = 19$, $R = 0.211$, $p > 0.05$).

Following the extraction of smolt data a comparison in growth between smolting (individuals classed as S2 and S3) and non-smolting trout (individuals classed as B & S1) was possible. The average size (cMFL) of individual one, two and three year old smolting and non-smolting trout sampled from each population is shown in Figure 3.8. This shows that in one year olds, smolting trout were on longer on average than same aged non-smolting trout. However, in two and three year old individuals, non-smolting trout were longer, on average. One-way ANOVA showed that in each case the difference was significant (Age 1: $F(1,273) = 21.742$, $p < 0.001$; Age 2: $F(1,215) = 10.968$, $p < 0.005$; Age 3: $F(1,30) = 18.722$, $p < 0.001$).

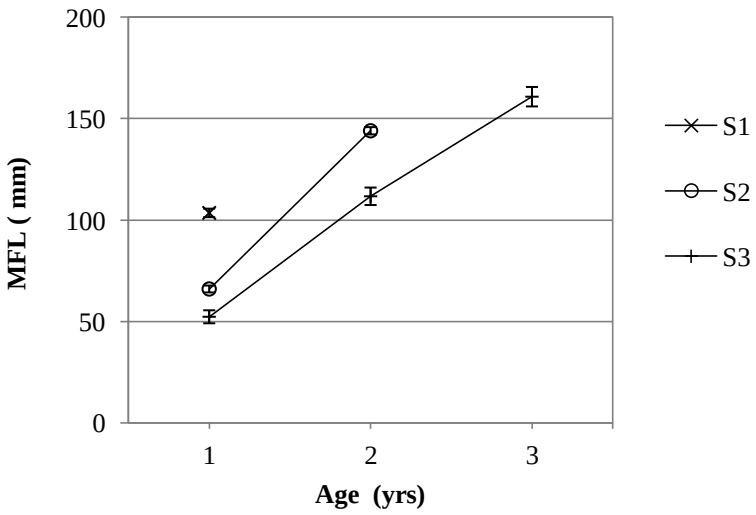
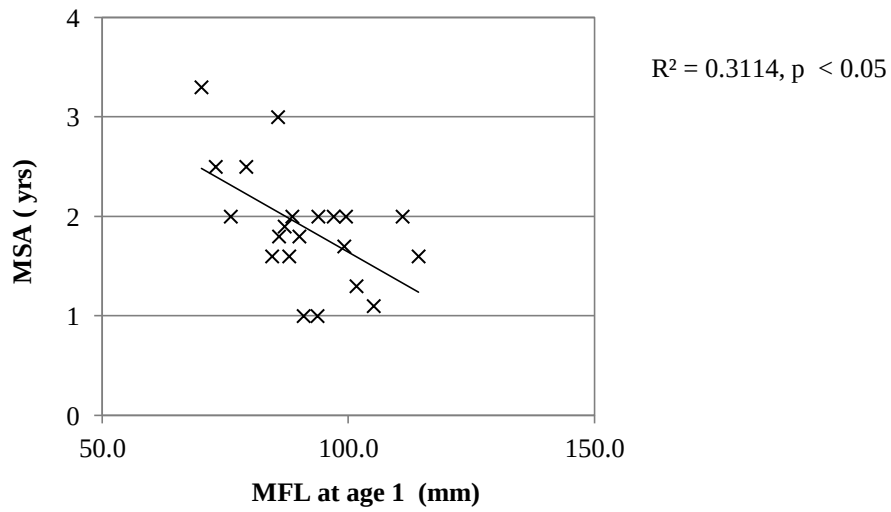


Figure 3.6: Orkney-wide growth curves for S1 (N=62), S2 (N=113) and S3 (N=15) smolts sampled from 21 Orkney burns, 2004 – 2009. Length at each age are representative of MFL (± se) at the end of each winter annulus.

a)



b)

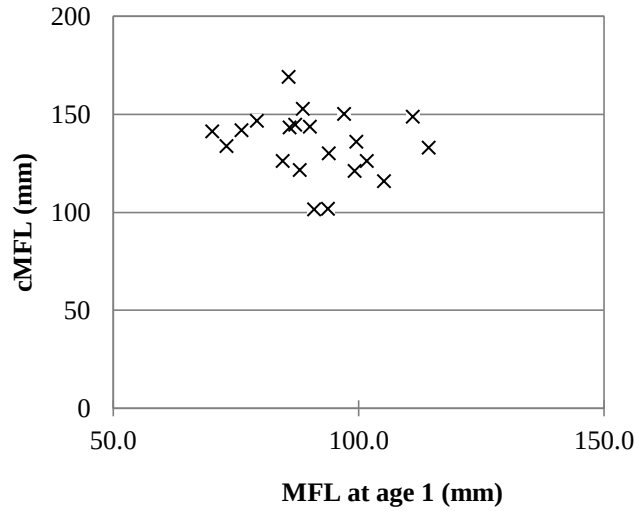


Figure 3.7: Relationship between mean first year growth and a) MSA (df = 19, R = 0.558, p < 0.05) *and b) cMFL (*df = 19, R = 0.211, p > 0.05) *in smolts (N=188) from 21 trout populations sampled in Orkney between 2004 and 2009.*

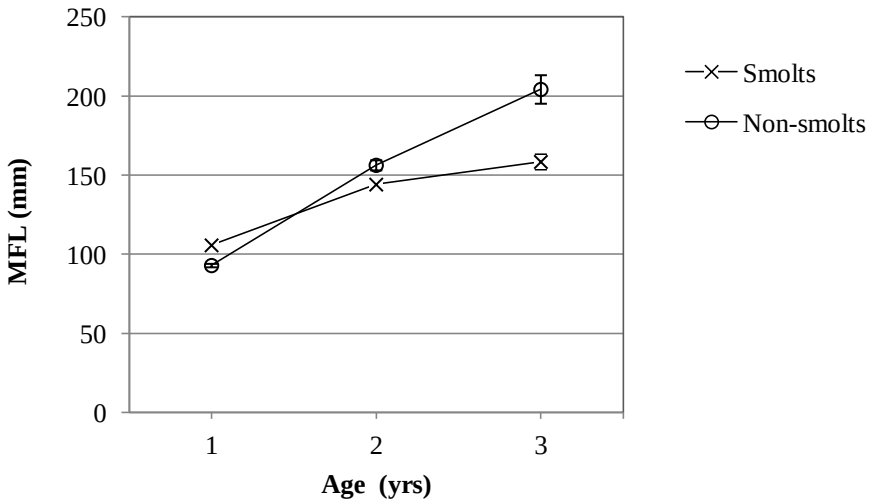


Figure 3.8: Comparison of size at age (cMFL ± se) between smolting trout (individuals classed as S2 & S3, sampled from 21 burns) and non-smolting trout (individuals classed as B & S1 sampled from 29 burns), 2004 – 2009.

3.3.4 B-growth in smolts

B-growth was observed on smolt scales as a widening of the circuli outside the last winter check and is illustrated in Figure 3.9. B-growth represented the increase in size achieved between the end of winter (cMFL) and the time of sampling (oMFL). The extent of B-growth exhibited by each age cohort in terms of length and weight increase is detailed in Table 3.6. B-growth resulted in an extra 28.0mm growth in S1 smolts, 17.5mm in S2 smolts and 11.0mm in S3 smolts. However the weight gain represented

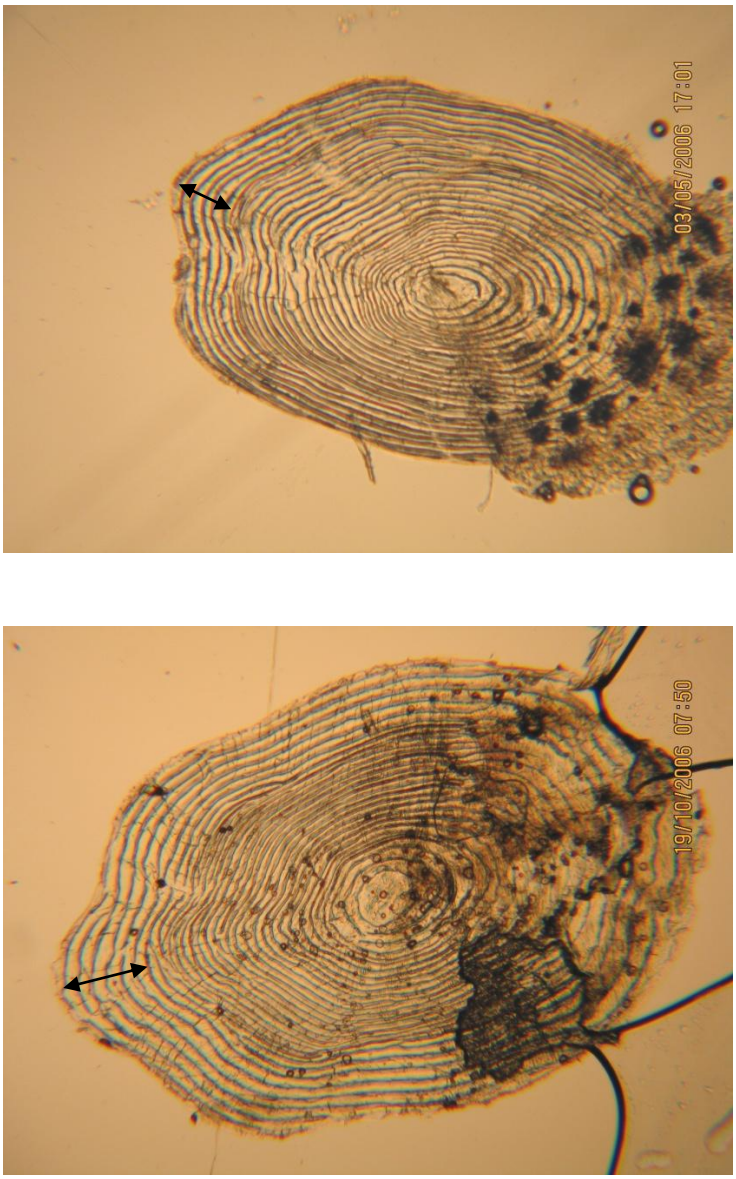


Figure 3.9: Examples of the B-growth phase (black arrow) in smolts sampled from the Eyrland burn: (top) an S2 smolt taken on 19th April 2006, (bottom) an S1 smolt taken on the 3rd June 2006.

Table 3.6: B-growth as the mean individual length increase between the end of the last winter annulus and the moment of sampling in different aged smolts sampled from 21 populations in Orkney, 2004 – 2009. Weight is estimated from the function y = 0.0056x2 - 1.0351x + 63.37, where y = weight in g and x = length in mm (Appendix F).

Smolt age (yrs)	N	cMFL (mm)	oMFL (mm)	Mean B-growth (mm)	Mean B-growth (g)
1	55	106.9 ± 2.4	134.9 ± 1.5	28.0 ± 2.0	8.0 ± 0.7
2	109	145.0 ± 1.8	161.1 ± 1.7	16.2 ± 1.2	10.8 ± 0.9
3	15	158.4 ± 4.8	169.4 ± 5.2	11.0 ± 2.2	9.2 ± 1.9

by this additional growth was similar between the three age cohorts, at approximately 8-11g. B-growth caused a reduction in size difference between different aged smolts prior to seawater entry. The difference in the MFL of S1 and S2 smolts reduced from 38.1mm at the end of the last winter annulus (cMFL) to 26.2mm at the point of sampling (oMFL). In similar terms, the difference between S2 and S3 smolts reduced from 13.4mm to 8.3mm.

Smolting trout exhibited greater B-growth relative to same-aged non-smolting trout. This difference was significant in one year olds ($F(1,261) = 14.589$, $p < 0.001$) and two year olds ($F(1,210) = 22.975$, $p < 0.001$). While three year old smolts also exhibited more B-growth that non-smolting individuals, the difference was not significant ($F(1,29) = 3.352$, $p > 0.05$).

3.3.5 Regional growth differences

A regional comparison was made between trout populations on the Orkney mainland and those on the island of Hoy. The comparison was made using only Scapa Flow populations (*i.e.* those inhabiting burns draining into Scapa Flow) of which there were 12 in total, with six on the mainland and six on Hoy. The location of each burn is shown in Figure 3.10.

On average, trout from the mainland burns were larger than same aged trout from the Hoy burns. The average size of all trout sampled in each group (including resident and smolting trout) is shown in Figure 3.11. One way ANOVA showed that mainland trout were significantly larger than same aged Hoy trout in each age group (1yr olds:

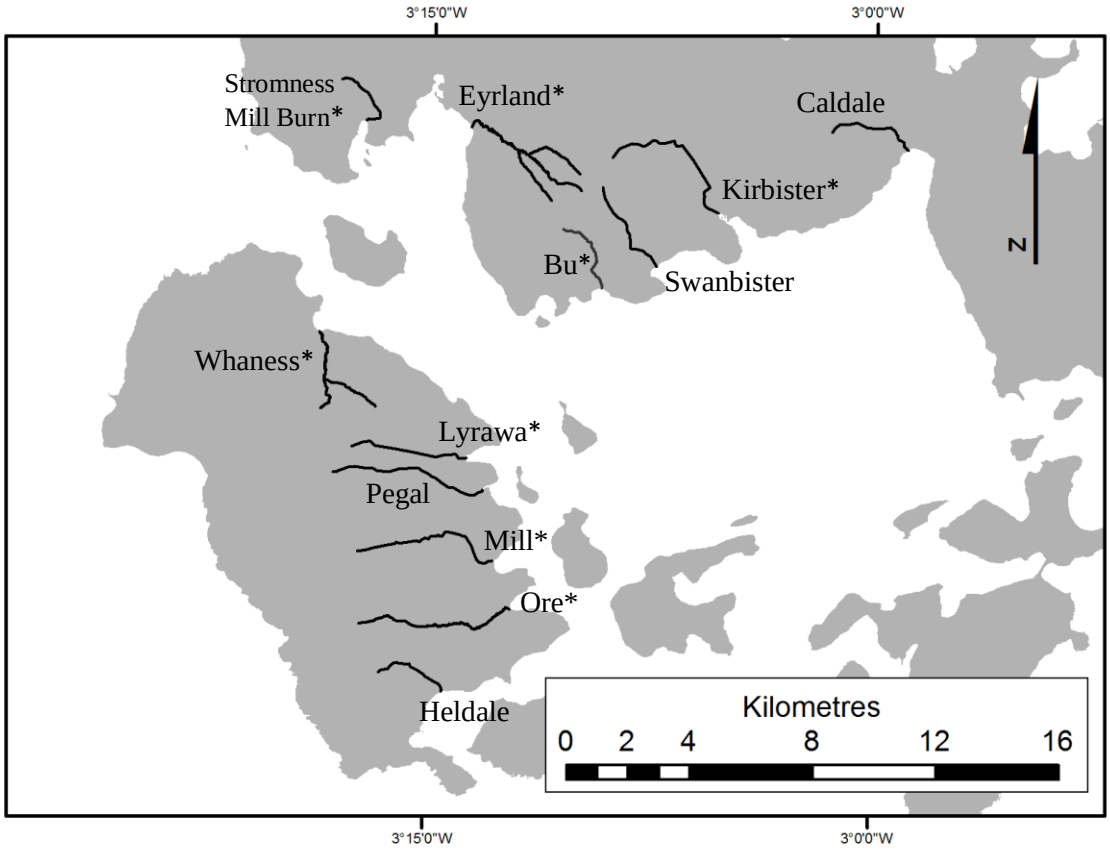


Figure 3.10: Map of Scapa Flow, showing the location of selected trout burns on the mainland and on the island of Hoy. Burns marked with a "" contain anadromous trout populations.*

F(1,212) = 21.083, p < 0.001; 2yr olds: F(1,120) = 18.338, p < 0.001; 3yr olds: F(1,20) = 22.234, p < 0.001). In the same 12 burns, smolts were found in four mainland burns and four Hoy burns. A summary of smolt data for each group is provided in Table 3.7. One way ANOVA showed that, across all age cohorts, there was no significant difference in smolt size (oFL) between the two groups (F(1,100) = 0.723, p > 0.05)) although mean smolt age was significantly higher in the Hoy group (1,100) = 37.963, p < 0.001). However, same aged smolts were significantly larger in the mainland group (Figure 3.12). One way ANOVA showed that both S2 and S3 smolts from the mainland burns were significantly longer than their Hoy counterparts (S2: F(1,56) = 8.837, p < 0.05; S3: F(1,12) = 9.944, p < 0.05). There were only four S3 smolts in the mainland group so this comparison would benefit from more data.

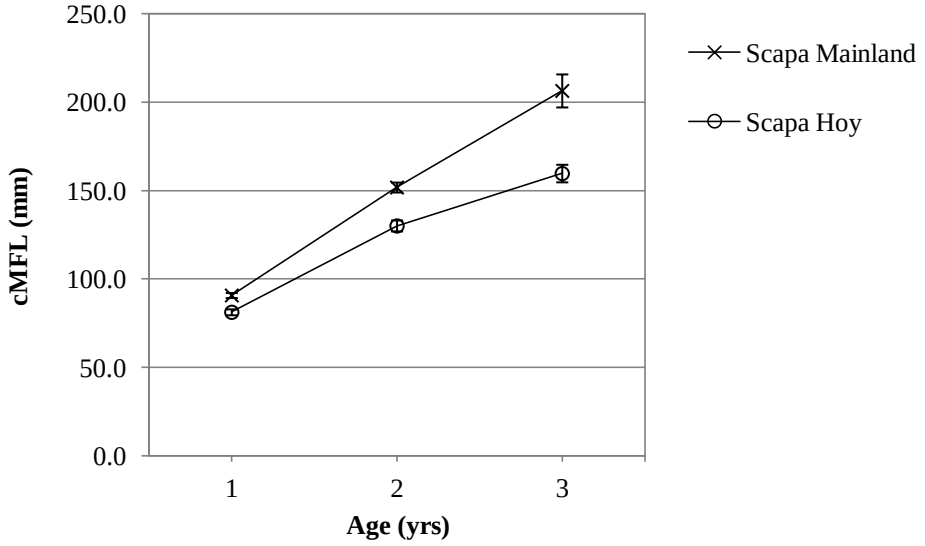


Figure 3.11: Comparison of cMFL (±se) of individual one, two and three year old trout (smolts and residents) sampled from six mainland burns and six Hoy burns draining into Scapa Flow, 2004 - 2009.

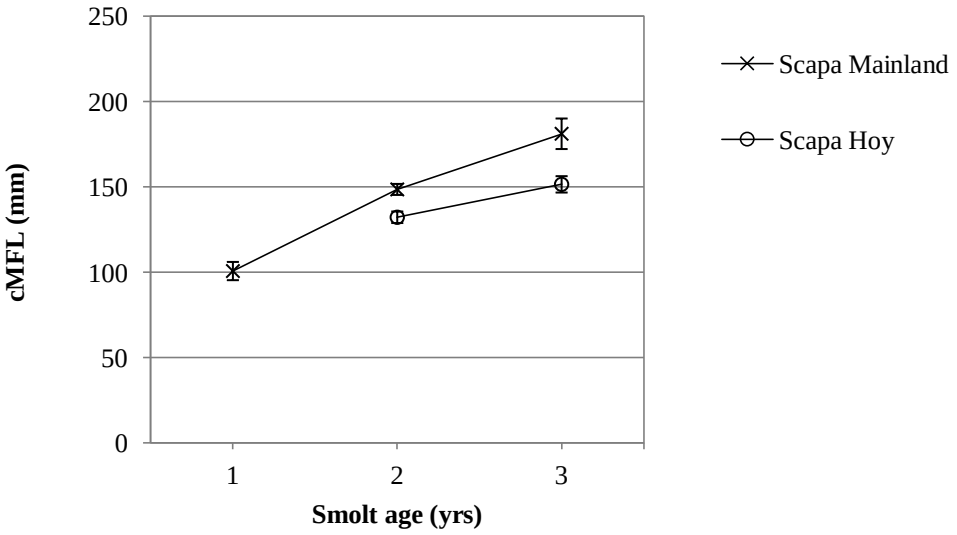


Figure 3.12: Comparison of pooled cMFL in S1, S2 and S3 smolts sampled from mainland and Hoy burns draining into Scapa Flow, 2004 - 2009. Length corrected by back calculation to the end of the last winter annulus.

Table 3.7: Comparison of oMFL between smolts sampled from mainland and Hoy burns draining into Scapa Flow, 2004 - 2009.

Group	No. burns	No. smolts	oMFL ± se (mm)	MSA ± se (yrs)
Mainland	4	75	155.2 (± 5.0)	1.6 (± 0.7)
Hoy	4	28	150.9 (± 4.0)	2.4 (± 0.7)

3.4 Discussion

This work represents the most extensive audit of coastal burns ever carried out in Orkney. Of 82 burns surveyed, brown trout were found in 36 separate watercourses. Evidence of anadromy was found in 23 of these populations. Over half the burns surveyed appeared to contain no trout. Samples mostly comprised immature and mature trout aged 0+, 1+ and 2+ in the freshwater stage of the life cycle. Growth rates varied between populations but also within populations as MFL declined with upstream distance. Mature resident fishes were also found and were predominantly male. Smolting trout were mostly aged two years with lesser numbers of S1 and S3 fish. Scale analysis revealed that younger smolts were faster growing but smaller at the point of migration than older smolts. B-growth was evident among smolts and was greatest on average among S1 smolts. A regional difference in growth rate was evident where trout from mainland populations were faster growing on average than those from populations on the island of Hoy. Faster growth in the mainland populations manifested in a younger MSA although MFL at smolting was similar.

A multitude of small waterways

A total of 23 anadromous trout populations were identified in Orkney. Many of the remaining 14 burns supported seemingly viable resident populations and evidence of anadromy may yet be found[1]. Such extensive regional studies are relatively rare in the UK. A total of 103 sea trout systems have been identified in the Outer Hebrides (OHFT, 2007). The MFSTP has identified number of burns around the Moray Firth, *e.g.* in the Beauly Firth and on the Black Isles which are existing or historical sea trout burns (MFSTP, 2011). Shetland, Orkney's nearest island neighbour, has numerous small burns but few formal surveys have ever been carried out (Watt, 2008; Thomson, 2010). Of the 36 burns found to support brown trout, the smallest was the Burn of Maitland which runs through the village of Finstown on mainland Orkney (HY 363136). Few formal estimates of water discharge exist for streams in Orkney. The discharge of the Maitland system has a catchment area of approximately 0.5km^2 and the

[1] Evidence of anadromous activity (smolts) was recorded in Boardhouse/Hundland system in spring 2010 by D. Brazier, OTFA. The trout inhabiting the linked lochs of Stenness and Harray almost certainly exhibit anadromous behaviour given the catches of sea trout made here each year but sampling efforts failed to find any evidence in the course of this project.

author estimates an average annual discharge of approximately 0.014cumecs [2]. The smallest burn to support anadromous trout was the West Rennibister burn, with catchment size of approximately 1.5km^2 and an estimated discharge of 0.048cumecs (based on the same calculation used for the Burn of Maitland). These two burns appear to be close to the lower size limit for the survival of trout populations, judging by a number of Scandinavian studies of anadromous trout. Jonsson *et al*. (2001) noted the presence of anadromous brown trout populations in two Norwegian streams with mean annual discharges of 0.04 & 0.05cumecs. Jonsson *et al.* (2011) examined 12 Swedish streams, including three with a catchment area of approximately 3km, all of which contained anadromous brown trout. Perhaps the most interesting comparison comes from the Baltic island of Gotland, which is analogous to Orkney in that it supports multiple populations of sea trout which spawn in small coastal streams. Limburg *et al*. (2001) studied three small streams there which supported anadromous trout, including one system of only 250m in length. While the catchment size and discharge rate is unknown, the stream was small enough to experience periodic droughts which wipe out or severely reduce the trout population. The sample of trout from the Maitland burn contained at least two age cohorts of trout (0+ and 1+) although no smolts were found there. The West Rennibister sample also contained two age cohorts of resident trout and while no smolts were found, two returning sea trout were found both of which were small (<250mm) mature females aged 1.1+. The presence of more than 1 age cohort of trout suggests that these two small burns had not experienced any severe drought recently. More detailed information on the water discharge rate and trout population in each burn would afford a better understanding of this situation but in the meantime, a marker (albeit an approximate one) is set for the minimum discharge required to support a brown trout population.

The presence of resident brown trout but absence of smolts observed in some Orkney burns may be the result of poor sea access. For example, the Caldale Burn on the mainland, running adjacent to the Scapa Distillery, contained a thriving resident trout population with the autumn sample comprising a number of mature female fishes, rarely

[2] Catchment size for the Maitland burn estimated by delineation of the drainage area in Google Earth as a polygon. The area of the polygon was calculated using a tool on the website www.earthpoint.us. Rainfall in Orkney is on average 900mm annually. Therefore, a total of 0.5km^2 x 900mm equals 450,000m^3 of water, which converted to an annual average flow equates to 0.014cumecs. This figure should be regarded as approximate as does not take evaporation into account or other factors which affect discharge such as slope and land use.

found elsewhere. Cooling water discharges from the distillery may raise the ambient water temperature in the burn. The discharge of distillery cooling water in the River Spey was thought to cause a local increase in freshwater growth rate in both Atlantic salmon and brown trout, which in turn led to earlier migration in salmon (Morrison, 1989). Interestingly, the Caldale Burn has a waterfall right at the beach, which probably prevents upstream access from the sea. It has been found that impassable barriers favour residency over migration in trout populations living upstream (Jonsson, 1982; Elliot, 1989). This burn therefore provides an unusual set of conditions for its trout population. Potentially warmer water might increase growth and encourage earlier migration, but the waterfall may select against a migratory lifestyle. The relatively high rate of mature females among the resident fishes sampled there suggests that residency may indeed be the preferred life-history tactic in this population. Further examination of this population would provide an interesting case study in itself.

A somewhat surprising result was the absence of trout from 44 of the burns surveyed. Anecdote suggests that at least some of these burns supported trout in the past. Some systems were clearly larger in terms of water discharge than some systems where trout were present (*e.g.* West Rennibister, Maitland), suggesting other factors were responsible for the absence of trout, such as poor sea access, excessive channel modification and pollution. The analysis of such parameters was beyond the scope of this study. The information in on presence/absence of trout populations in a large number of Orkney burns provides the basis for a more detailed investigation of physic-chemical parameters in freshwaters and their role in supporting or excluding trout populations. Such a study would also serve as a basis for habitat improvement work with the aim of (re-) introducing trout to burns where they were present historically.

Growth and density

Growth estimates in some cases were based on relatively small sample sizes, so should be treated with caution. Furthermore, the samples were collected in different years when growth conditions may have differed. Despite these drawbacks, the growth analysis suggested some interesting trends and directions for future research. Previous research on the growth of brown trout populations in Orkney is limited to one study (Figure 3.13). Duncan *et al*. (1992) estimated mean annual growth in brown trout from

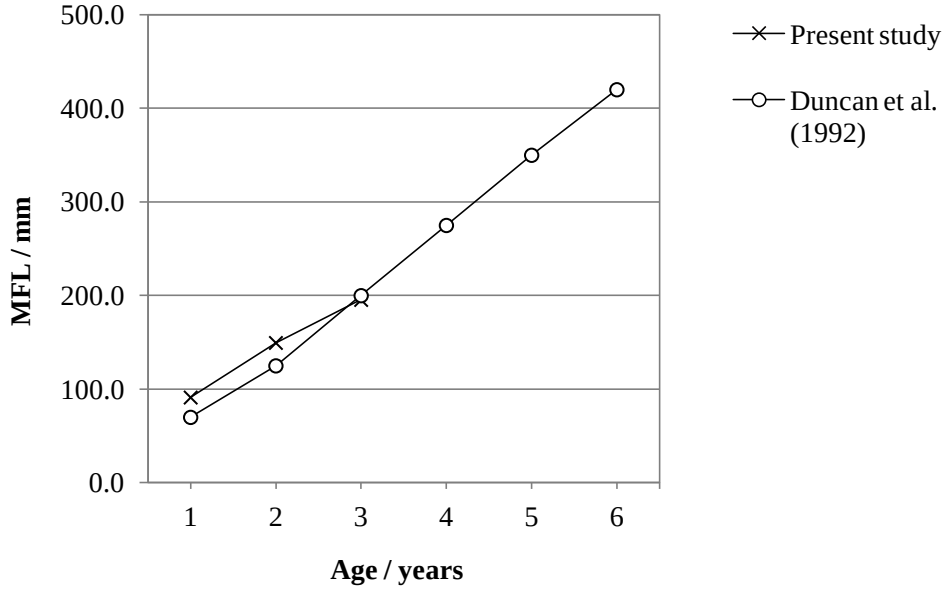


Figure 3.13: Comparison of the overall growth curve (based on immature and mature resident trout & smolts) sampled during the present study with the Orkney mean calculated by Duncan et al. (1992).

Orkney's five major lochs, based on gill-netted trout samples. The present study showed a deceleration in growth between years two and three. In contrast the results from Duncan *et al*. (1992) showed that relatively steady growth was maintained year on year in fishes up to six years old. This possibly reflects the better growth opportunities in loch habitats relative to burn habitats, where the decrease in growth rate reported here could be expected. This comparison should be made with some caution however, as the data contained in this chapter are limited and growth estimates were based on empirical (direct) observation of each age cohort, while the growth data contained in Duncan *et al*. (1992) were based on back calculation, which can result in the under-estimate of length at younger ages, in an effect known as the Rosa Lee phenomenon (Lee, 1912). Comparisons with growth data from other regions of Scotland are problematic for the same reasons. It could be noted however that growth curves for one and two year old trout in the Loch Leven system were similar to that seen here (Armstrong *et al*., 1994).

Inter and intra-burn comparison

Single run (semi-quantitative) surveys carried out in the burns of Eyrland, Bu, Isbister and Rossmyre in 2005 provided more detailed information on the population in each burn and therefore allowed a more confident comparison between populations. Two measures of CPUE were available in this phase of work, number of trout per unit area

Table 3.8: Summary of juvenile trout densities (number 100m^{-2} for rivers of <4m width) based on one-run electrofishing events at sites throughout Scotland. Minimum, maximum and quintile points are shown. Quintile ranges are calculated from those sites with densities greater than zero, the percentage of sites with zero density is indicated. From Godfrey (2005).

Age cohort	Quantile	Density (100m^{-2})	Classification
0+	0th percentile	0.6	E
	20th percentile	4.5	D
	40th percentile	11.0	C
	60th percentile	22.9	B
	80th percentile	49.9	A
	100th percentile	415.7	-
	Percent zero density	12.9	-
1++	0th percentile	0.7	E
	20th percentile	4.5	D
	40th percentile	5.0	C
	60th percentile	8.3	B
	80th percentile	15.3	A
	100th percentile	174.2	-
	Percent zero density	15.2	-

(100m^2) and catch min^{-1}. The area based results, when compared to the FCS classification scheme (Table 3.8) suggested high density in both 0+ and 1++ trout at some sites in each of the four burns. However, the average density of trout at all sites in each system was more modest and scored from "A"to "C" (0+) and from "B" to "D" (1++). Given the more extensive nature of the semi-quantitative data, it is reasonable to conclude these are more accurate assessments of the trout population in each system for that particular year (2005). Based on the timed electrofishing standards used by the Wester Ross Fisheries Trust (Table 3.9), density at the four burns were moderate to high on average.

Growth of 0+ trout was fastest in Isbister, followed by Eyrland, Bu and Rossmyre. This is slightly different from the rank suggested from the presence/absence survey data, illustrating the limitations of that dataset. The timed surveys also showed that as well as density, growth of 0+ trout could vary significantly between different sites in the same burn. The presence of the slowest growing 0+ trout at the furthest upstream site in each of the four burns may be related to reduced flow rates, space and food, relative to sites

Table 3.9: Classification of fish density based on timed electrofishing data (Wester Ross Fisheries Trust, 2010)

Fishes caught min^{-1}	Grade
0	Absent
0.1 – 0.5	Very low
0.6 – 1.0	Low
1.1 – 2.0	Moderate
> 2	High

further downstream. Colder water temperatures in upstream areas can result in reduced growth (Shackley & Donaghy, 1992). However, the four burns in the present study are only several miles long at most and do not climb more than 150m above sea level, so it is unclear if significant temperature changes could still occur over such short distances.

Single run surveys also provided useful data on mature resident trout and returning sea trout in each of the four burns. Among resident trout there was a clear sex bias towards male fishes, reflecting the tendency for males to reside in freshwater and females to migrate to sea, as reported elsewhere (Campbell 1977; Pratten & Shearer, 1983a; Jonsson 1985; Euzenat *et al*. 1999; Jonsson *et al*. 2001). The comparison of growth between same aged mature and immature resident trout did not show any consistent trend and would benefit from more extensive data. The literature reports that the growth rate of mature resident trout can be faster than, slower than or similar to migratory fishes (Jonsson, 1985; Elliot, 1994). In this case the assumption was made that immature fishes would go on to smolt and migrate which clearly may not be the case, so more a more careful comparison with additional data is required before making any firm conclusions here. Sea trout comprised finnock and one sea winter (SW) trout, some of which carried salmon lice (*Lepeophtheirus salmonis*) indicating their recent arrival from the sea. Most of the one SW trout were female, while most of the finnock appeared to be male. The Eyrland sample contained two VIE tagged trout (red tag, right eye), indicating they had been tagged by the author as smolts leaving that burn in spring 2004, illustrating a degree of faithfulness among Orkney sea trout to their natal burn.

Smolt characteristics

Analysis of smolt data also highlighted differences in growth dynamics between burns supporting anadromous trout populations. However, some of the same caveats apply

here when making conclusions based on discrete samples. Smolt characteristics may vary from year to year but perhaps more significantly, at different stages through the spring migration window which typically lasts two to three months. Bohlin *et al*. (1996) showed that smolt MFL declined through the spring period, so the timing of sample collection clearly has the potential to affect the estimation of factors such as MFL in emigrating smolts. In addition, it must be acknowledged that given the sampling method employed in this part of the project, some smolts could have been to sea and achieved some marine growth prior to sampling, which would inflate estimates of smolt growth achieved in freshwater. In general there were no external indicators of marine residency, *e.g.* external marine parasites. For the moment, the assumption is made that smolts sampled in this phase had not been to sea but this issue will be examined later in chapters 5 & 6 where smolt growth is studied in more detail.

The smolts sample was sufficient to provide a broad understanding of smolt characteristics across Orkney. Average smolt size (152.2mm) and age (1.9 yrs) estimated in the present study were less than those estimated by Nall (1933) in the Graemeshall (172.1mm, 2.3yrs) and St Mary's (166.8mm, 2.3yrs) populations on the east mainland of Orkney. The individual results for the Graemeshall burn in this study were also less than the historical estimates. While Nall (1933) found no S1 smolts in either of the two burns, the present study found numerous S1 smolts in the Graemeshall system, suggesting that the nature of the smolt run here may have changed, although additional survey work is required to know for sure. It is relevant that both systems were being stocked with fry at the time of Nall's study, which may have had an effect on subsequent smolt length and age. The failure during this study to find any smolts and only very few resident trout in the St Mary's system suggests a dramatic decline in the trout population in this burn and further investigations are also required there.

Smolts in Orkney were also smaller and younger on average when compared to contemporary data from other Scottish systems (Table 3.10). While the relatively limited nature of the Orkney dataset should be considered, it is worth noting that Nall (1933) made the same observation when comparing his Orkney data to those from his numerous other studies across Scotland. It is generally assumed that MSA increases with latitude increases (Euzenat *et al.*, 1999; Jonsson & L'Abée-Lund, 1993), an impact of decreasing water temperatures on growth. However, Orkney appears to produce younger smolts on average than populations in more southern parts of Scotland. Why

Table 3.10: MFL and MSA in sea trout smolts samples from other Scottish rivers.

System	Year	MSA (yrs)	MFL (mm)	Reference
Shieldaig	2002	-	158	McKibben & Hay (2002)
	2004	-	176	McKibben & Hay (2004)
	2007	-	171	Raffell, Buttle & Hay (2007)
North Esk	1976	2.19	175	Pratten & Shearer (1983a)
	1977	2.11	166	
	1978	2.21	168	
	1979	2.44	169	
	1980	2.25	175	
Tournaig	1999	3.0	167	Wester Ross Fisheries Trust (2001)
	2000	3.1	190	
	2001	2.8	189	

might this be the case? The fact that smolts in Orkney are younger on average compared to other Scottish populations, suggests that freshwater growth rate in Orkney trout is faster, resulting in migration at a younger age. This is perhaps not surprising given Orkney's relatively mild climate, fertile landscape and productive freshwaters, previously described in Chapter 2, which might easily result in relatively fast freshwater growth relative to other Scottish systems.

Examination of smolt growth provided several interesting results. Faster freshwater growth led to a younger age at smolting on average. There were significant differences in first year growth between S1, S2 and S3 smolts. Similarly, the size of S2 smolts was larger on average than S3 smolts when aged two. Smolt size however increased with age. These findings reflect those of other studies (Jonsson & L'Abée-Lund, 1993; Økland *et al.*, 1993; Toledo *et al.*, 1993; Euzenat *et al.*, 1999) and demonstrate that both fast and slow growing individuals can smolt successfully. An interesting component of this trend was the fact that S3 smolts were similar in size at two years old to S1 smolts at one year old. This result was also noted by Økland *et al.* (1993) in a Norwegian population of anadromous brown trout and was used to refute the notion that smolting accords to a threshold size. The inverse relationship between mean first year growth and MSA in the study populations has not been noted previously (Jonsson & L'Abée-Lund (1993) noted the a similar relationship between the second year growth increment and MSA). It is noteworthy that this relationship appears to occur on such a local scale,

and serves to highlight the range of growth rates exhibited among the anadromous trout populations identified during this study. Furthermore, the comparison of growth between same aged smolting and non-smolting trout showed that smolts can be faster or slower growing than same aged resident individuals, agreeing with the results of Jonsson (1985). The fact that smolts can exhibit a wide range of growth rates and may be either faster or slower growing than resident individuals serves to underline the complexity of migratory behaviour in anadromous brown trout populations. Again, more data would be helpful here to better describe this characteristic in Orkney trout populations.

B-growth was frequently observed on smolt scales sampled from April onwards and was significantly greater than average plus growth in same aged non-smolting trout. The spacing of circuli in this spring period was wider than in previous summer growth phases. This apparent acceleration in growth is typically associated with the change to a marine diet and is sometimes referred to as "run-out" (Elliot & Chambers, 1996). However, all these smolt samples were taken in freshwater and there were no external indicators of marine residency, *e.g.* parasites such as *Lepeophtheirus salmonis* or *Cryptocotyle lingua*. As mentioned previously, it is possible that smolts had been to sea but returned to freshwater when they were sampled. However, it is also possible that B-growth could have occurred in freshwater prior to entering the sea, perhaps by voracious feeding or tissue re-modelling in preparation for migration (Hoar, 1988). Freshwater B-growth (reported as "plus growth") was noted by Pratten & Shearer (1983a), particularly among younger smolts, but not until June. In terms of increase in FL, B-growth was greatest in S1 smolts and declined with age, reflecting findings made elsewhere in Scotland and Ireland (Went, 1949; Fahy, 1981; Pratten & Shearer, 1983a). As younger smolts tend to be smaller than older smolts (within populations) the ability to undergo a late surge in growth allows them to catch up in size terms with older (larger) smolts which exhibit less B-growth on average. This suggests two interesting notions. Firstly, a greater need in smaller smolts to maximise size prior to seawater entry which might be used as evidence to support the presence of a threshold smolt size in anadromous brown trout, the existence of which is refuted by some authors (Økland *et al.*, 1993). Secondly, if B-growth indeed varies inversely with smolt size, then B-growth might be seen as a type of compensatory growth phase, following a period of reduced growth, as seen in laboratory experiments involving other salmonids (Nicieza & Metcalfe, 1997). Again this thesis would benefit from additional data and more

detailed analysis of B-growth among smolts and its relevance to size at migration follows in later chapters.

Regional variations

As well as differences between individual systems, it was also clear that regional differences in freshwater growth rate existed within Orkney. This was illustrated neatly by the comparison of the mainland and Hoy burns draining into Scapa Flow. The relatively slow growth rates measured in the Hoy trout populations resulted in smolts which, although similar in size, were significantly older on average than their mainland counterparts. This might be used to support the notion of a threshold size in sea trout populations (Fahy, 1985), but it might equally be used to support the view that brown trout have different energetic requirements and smolting results only when an energetic bottleneck occurs (Forseth *et al*., 1999). Without further data on this issue, one can only speculate on why growth rates in Hoy trout populations were slower relative to those on mainland Orkney. Growth among Hoy trout did not appear to be limited by high population density. Hoy and mainland Orkney lie on opposite ends of Orkney's agricultural spectrum. Hoy (meaning "high" in Old Norse) has been largely unaffected by modern agriculture largely due to its topography. Despite the underlying sandstone geology, extensive peat deposits result in some particularly acidic conditions in its lochs, where ph values of less than 5 have been recorded (Duncan *et al.*, 1992). It is likely therefore that Hoy's running waters also experience acidic conditions, which may adversely affect trout growth and survival (Alabaster & Lloyd, 1982; Solbé, 1988). The Orkney mainland, in contrast, is low lying and dominated by intensive agriculture. Peatland has been converted to grassland and artificial fertilisers are used to maximise production of grass. Mainland lochs are exclusively alkaline and at least moderately enriched as a result. Despite extensive morphological manipulation to the mainland's running waters, conditions seem to support both faster growth and higher densities of trout than Hoy's "pristine" burns.

Summary

To recap, the work described in this chapter represents an extensive study of the numerous coastal burns in the Orkney Islands. Brown trout were found in 36 separate watercourses of the 82 surveyed. All age cohorts up to the age of 5+ years were found

although most fishes were aged between 0+ and 3+. Trout density varied between burns and ranged from very low to very high and growth rate also varied between populations. Growth rates also varied within populations as MFL was found to decline with upstream distance. Mature resident trout (non-anadromous) were also found and were predominantly male. Evidence of anadromous behaviour (the presence of smolts) was found in 23 burns. Smolting trout were mostly S2s with lesser numbers S1s and S3s. Scale analysis revealed that younger smolts were faster growing but smaller at the point of migration than older smolts. B-growth was evident among smolts and was greatest on average among S1 smolts. A regional difference in growth was observed where freshwater growth was faster on average in populations on mainland Orkney relative to those on the island of Hoy. Faster growth in the mainland populations manifested in a younger MSA although MFL between the two groups of smolts was similar. The results provide a valuable management tool for future conservation of anadromous trout populations in Orkney as well as a sound basis for more detailed ecological investigations. The following chapter examines the regional difference in growth between trout populations on the Orkney mainland and the island of Hoy, by extension of the semi-quantitative electrofishing methodology.

CHAPTER 4. FRESHWATER GROWTH AND INCIDENCE OF MATURE RESIDENTS IN FOUR ANADROMOUS BROWN TROUT POPULATIONS

4.1 Introduction

Anadromous populations of brown trout (*Salmo trutta* L.) inhabit a range of freshwater environments, from tiny streams to large lake/river systems (Jonsson & Jonsson, 2006). Populations comprise individuals that migrate to sea before returning to freshwater to spawn (as sea trout) and individuals that grow and achieve maturity without ever leaving freshwater. A traditional view asserts that freshwater systems with low productivity encourage migration (*e.g.* Northcote, 1978; Gross *et al*., 1988; L'Abée-Lund *et al*., 1990). A more modern view recognizes a range of alternative migratory tactics (AMTs) in salmonids and hypothesizes that individuals within a population may follow any of the alternative tactics available to them (Dodson *et al*., 2012). Consequently, a fundamental question in brown trout research is what factors influence the choice between migratory tactics (Milner *et al*., 2006). As described in chapter 1, body size is often used as a liability trait in to explain migratory behaviour in salmonids (Aubin-Horth & Dodson, 2004; Thériault *et al.*, 2007; Piché, Hutchings & Blanchard, 2008). Therefore, environmental factors which control growth will also influence life-history decisions in brown trout populations.

Growth in juvenile salmonids is determined by a number of factors. Perhaps chief amongst these is water temperature, which is largely responsible for the broad geographic trends in population characteristics with exist across the native range of brown trout (Jonsson & L'Abée-Lund, 1993). Growth occurs within a temperature range of approximately 4°C to 25°C, with an optimum of between 15°C and 17°C depending on the size of the food ration (Elliott, 1995). Food intake, particularly in juvenile trout, depends on the availability of aquatic and terrestrial invertebrates, which in turn depends on water chemistry, water flow, habitat type and land use in the surrounding catchment. Invertebrate abundance and therefore food availability can be naturally greater in streams with suitable geology and also in streams which are semi-enriched by adjacent agricultural activity (Jonsson *et al.*, 2011). Water chemistry may also directly affect growth in salmonid fishes. Water pH of below 5.0 and above 9.0 can be harmful and the presence of certain dissolved materials, for example ammonia,

nitrites and aluminium, may also be detrimental in sufficient quantity (Alabaster & Lloyd, 1982; Solbé, 1988). Moreover, the toxicity of certain compounds can be modified by pH (*ibid*). Finally, stream size may affect growth in juvenile trout. Small streams can offer limited feeding and territorial opportunities for juvenile trout, the effect of which can be exacerbated by very low water flows. Some authors suggest that in very small streams, which are affected by drought, anadromous trout migrate to sea at an earlier age than those in larger streams (Jonsson *et al*., 2001; Landergren & Vallin, 1998). It is unclear if this is a response to adversity and limited food intake or a local adaption to such conditions. The effect of trout density on growth is unclear. An indirect relationship between density and growth has been reported by some (Backeil & Le Cren, 1967; Mortensen, 1977; Vøllestad & Forseth, 2002; Olsson *et al*., 2006) but refuted by others (Egglishaw and Shackley, 1977; Mortensen *et al*., 1988).

Many studies have assessed migratory behaviour within and between brown trout populations against growth performance in freshwater. In general, growth performance is measured against a single parameter, *e.g.* latitude or stream size. It is also important to distinguish two types of comparison which exist in the literature. The first type looks at the growth rate among trout which smolt at different ages. In this case it is important to appreciate that migration is the end result for all age cohorts. It is generally reported that faster growing fishes migrate at a younger age and a smaller size than slower growing fishes (Forseth *et al*., 1999; Økland *et al*., 1993). The second scenario, which is relevant to this chapter, compares growth between trout which exhibit varying degrees of migratory behaviour. Results vary. In the Vangsvatnet lake, Norway, Jonsson (1985) found that mature resident trout (male and female) grew within the range of growth exhibited by smolts, *i.e.* slower than younger smolts and faster than older smolts. Forseth *et al*. (1999) observed that among 3+ trout in a stream feeding a large Norwegian lake, mature male residents were larger than same aged lake migrants, but this was based on very limited data. Another study to suggest that fast growth stimulates residency and maturity was carried out by Olsson *et al*. (2006) who found that low density and higher growth rates (in terms of mass) of trout at a site above a waterfall resulted in a greater rate of residency and maturity relative to the downstream site, where individual density was higher and growth rate slower. In contrast, Bohlin *et al*. (1994) found that mature male resident grew more slowly than smolts. Therefore, no consistent pattern appears to exist in the relative growth rates of freshwater resident and

anadromous trout. The effect of stream size on the relative growth rate between resident and anadromous trout has not been considered.

A clearer relationship exists between growth rate and smolt age. Populations with higher growth rates tend to have younger smolts on average and due to the effect of decreasing temperature, mean smolt age tends to increase with latitude (Jonsson & L'Abée-Lund, 1993). Work in Norway also suggests that smolt age is lower and size is smaller in very small streams (Jonsson *et al*., 2001). However, the extent of this effect is difficult to distil due to the possibility of concurrent latitudinal, *i.e.* temperature, effects as the study involved streams spread over a distance of 300 miles from north to south. The effect of stream size might be more effectively assessed in streams at similar latitudes.

In salmonid populations which exhibit partial migration, those fish which reside and mature in freshwater are often dominated by males although in some cases the sex ratio may be equal (Campbell, 1977; Theriault & Dodson, 2003; Theriault, Bernatchez, Dodson, 2007; Morita & Nagasawa, 2010;Johnstone, O'Connell, Palstra & Ruzzante, 2013; Ohms *et al*., 2014). The characteristics of freshwater residents have been examined in relation to growth conditions within and between populations, but again, contrasting results have been reported. L'Abée-Lund *et al*. (1989) reported that between populations of anadromous brown trout, the frequency of mature male residents increased with freshwater growth rate. However, Dellefors & Faremo (1988) found no such relationship although they did report that within populations, the frequency of mature male residents varied between years, increasing in good growth years and *vice versa*. Jonsson *et al.* (2001) also found that the size and mean age at maturity in resident males increased with stream size, although as mentioned earlier, the potential effect of changing temperature was not considered.

There are conflicting accounts of growth attributes of migrant and resident trout in anadromous populations. There is a need to further test growth attributes in relation to specific environmental parameters, in a way which filters out other possibly significant growth factors. The extensive survey work described in Chapter 3 provided a broad view of growth patterns in numerous trout populations existing in separate watercourses across the Orkney Islands. While contrasting growth performance was observed between mainland populations, more significant differences appeared to exist between

populations inhabiting burns on the island of Hoy and on the Orkney mainland. This chapter develops this regional comparison by focusing on two anadromous trout populations in each group, four in total, over a three year period. The aims of this chapter were to answer the following questions:

- Is freshwater growth in Hoy populations slower than that in mainland populations;
- Is the trend of decreasing MFL with upstream distance a consistent feature in the sample populations;
- Does trout density, stream size or water temperature have a significant effect on freshwater growth;
- What is the frequency of mature resident trout in each population and is this affected by factors such as freshwater growth rate and stream size; and
- Is freshwater growth of mature resident trout faster than that of same-aged immature trout.

It was hoped that the relative close geographic proximity of the four populations would help to minimise the effect of varying latitude and temperature on this investigation.

4.2 Methods

Two burns each on mainland Orkney and the island of Hoy were sampled over a three year period (2007 – 2009). The mainland group comprised the burns of Eyrland and Bu. The Hoy group comprised the burns of Ore and Whaness. All four burns drain into Scapa Flow, their mouths being within 11km of each other (see Figure 4.1). Locations and catchment details are shown in Table 4.1. The catchments of Eyrland and Bu comprise a mixture of intensive agriculture, mainly confined to the downstream areas, with heather moorland and rough grassland dominating the upstream areas. In contrast, the catchments of both Hoy burns are almost completely dominated by heather moorland with some rough grassland in the lower reaches.

4.2.1 Sampling

In the autumn of 2007, 2008 and 2009, semi-quantitative (single run, timed) electrofishing surveys were carried out at multiple sites along the length of each burn

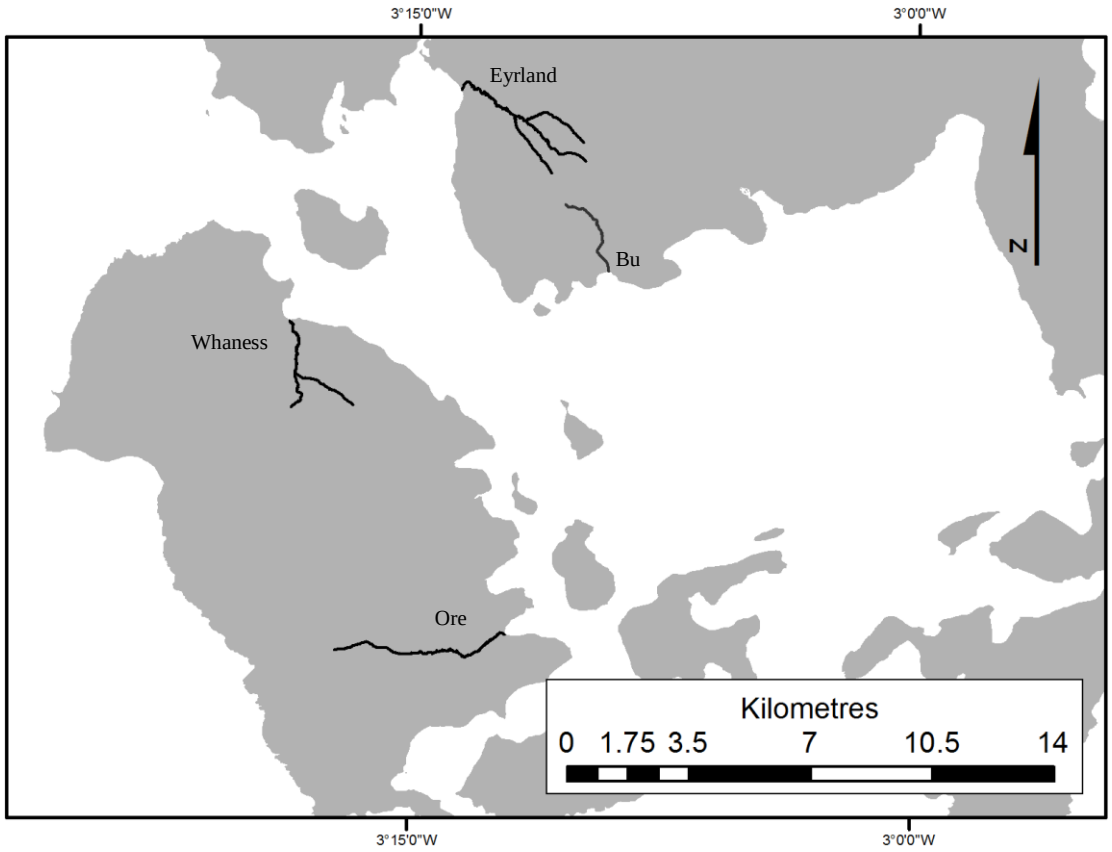


Figure 4.1: Map of Scapa Flow, Orkney, showing the location of the Eyrland, Bu, Ore and Whaness burns.

Table 4.1: Catchment details for the burns of Eyrland, Bu, Ore and Whaness. NGRs relate to burn mouths. Length estimates for main tributaries only. Discharge is annual mean water flow. Catchment and discharge data kindly supplied by the Scottish Environment Protection Agency.

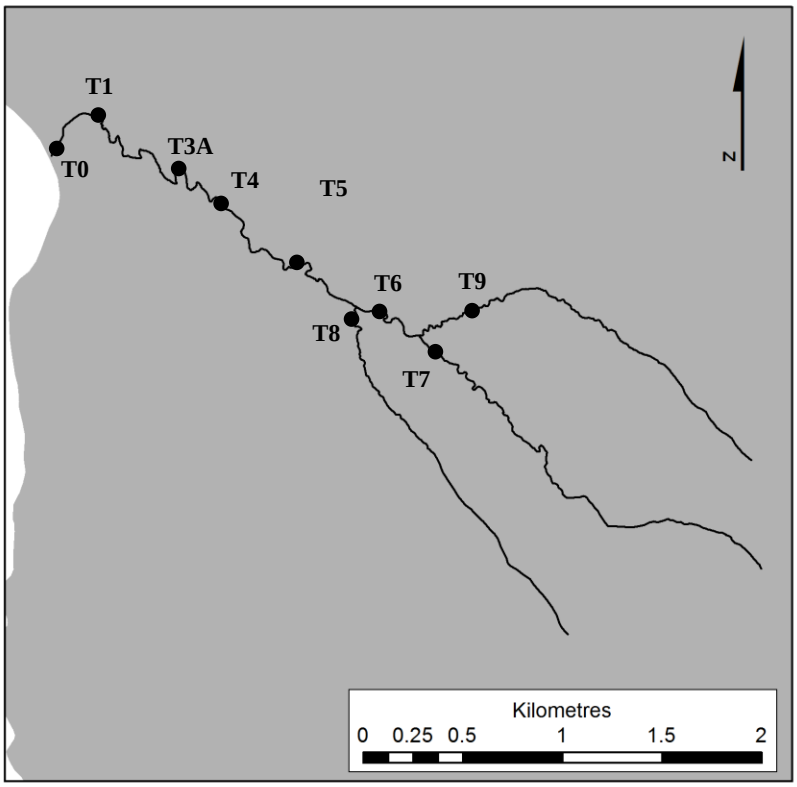
Burn	NGR	Length (km)	Mean altitude (m)	Max altitude (m)	Discharge (cumecs)	Catchment area (km^2)
Eyrland	HY 293 095	10.01	64.9	144	0.176	8.132
Bu	HY 335 043	4.51	46.1	140	0.068	3.404
Ore	ND 305 938	7.01	41.9	111	0.138	7.956
Whaness	HY 244 027	7.2	55.8	241	0.068	5.279

from the tidal limit to the upper reaches (Figure 4.2). Co-ordinates for each sample site are provided in Appendix G. Sampling time at each site varied from 10 to 20 minutes depending on the number of trout caught at each site. Surveys were carried out from late September to mid October where possible, although high water levels meant that some were delayed until early November. The semi-quantitative survey methodology was described previously in Chapter 2.

4.2.2 Fish processing

All fish samples were processed according to the procedure described in Chapter 2. .

Eyrland



Bu

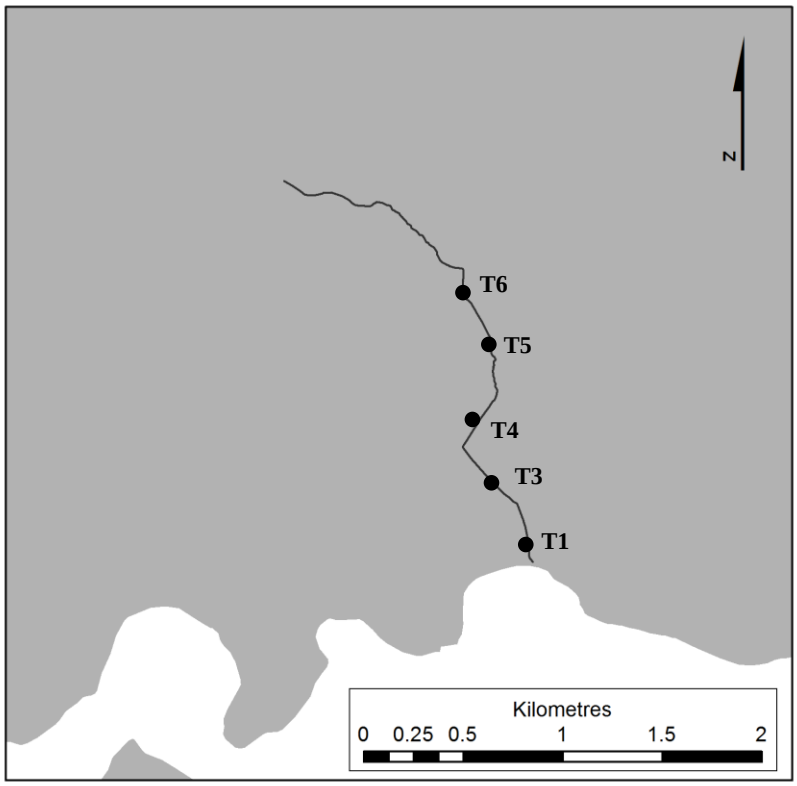
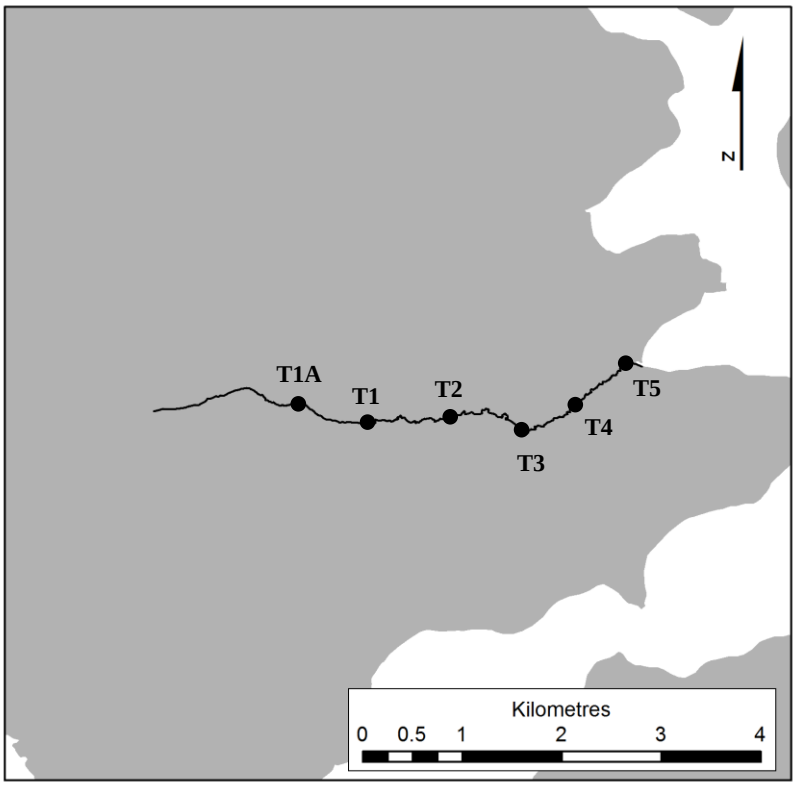


Figure 4.2: Location of timed survey sites on the burns of Eyrland & Bu, Ore and Whaness, sampled in autumn 2007 – 2009 (continued on next page).

Ore



Whaness

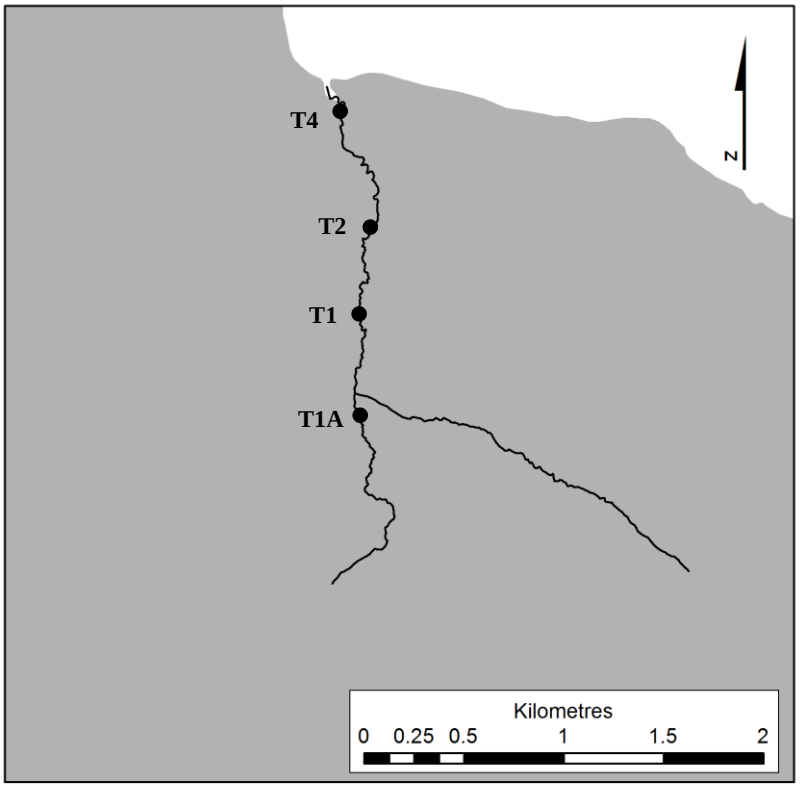


Figure 4.2 (continued): Location of timed survey sites on the burns of Eyrland, Bu, Ore and Whaness, sampled in autumn 2007 – 2009.

4.2.3 Temperature monitoring

Water temperature in each burn was recorded using Gemini Data Loggers (TinyTag Plus). The logger units were installed in the lower reaches of each burn, above any tidal influence. To anchor the loggers to the streambed they were fixed to a 2kg lead weight. This assembly was then tied to a bankside anchor point to ensure the logger was not swept away during high flows. Initially, the logging units were set to record water temperature at 6 hour intervals but this was subsequently changed to one hour intervals. They were downloaded using a direct serial cable connection to laptop using Gemini Logger Manager (V2.2). The logger units were regularly inspected and maintained throughout the survey period.

4.2.4 Scale reading

Scale reading was carried out as described in Chapter 2.

4.2.5 Data analysis

Data analysis was carried out using SPSS, versions 14 and 16. Comparison of fork length data was carried out using ANOVA. A p-value of 0.05 was used unless stated otherwise. Where more than two groups were being compared a post-hoc test (Fisher's LSD) was used to identify significant differences between the mean values of individual groups. Regression analysis was carried out using Microsoft Excel. Correlation was assessed by comparing the R-value from regression analysis to the Pearson product moment correlation coefficient for 2-tailed test.

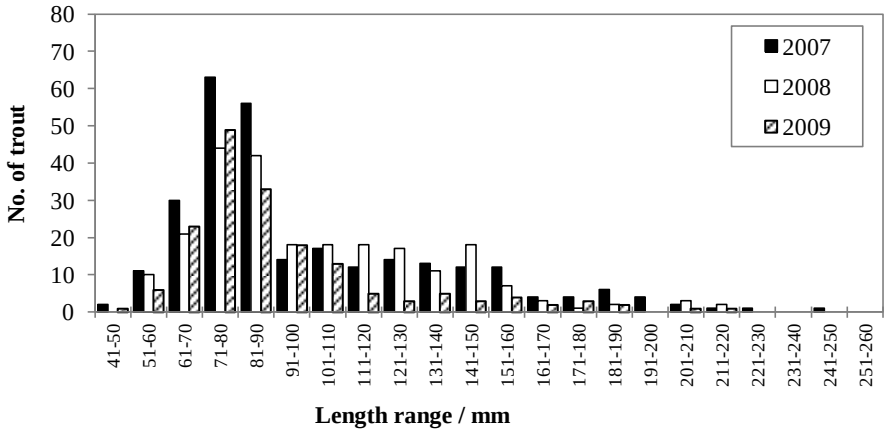
4.3 Results

A total of 1922 trout were sampled from the burns of Eyrland, Bu, Ore and Whaness over the three year sampling period. Annual sampling dates and effort are shown in Table 4.2 and a breakdown of the annual catch by age is provided in Table 4.3 for each burn. Individual survey results for each site on each of the four burns are detailed in Appendices H - K. The largest samples were obtained from the mainland burns which yielded a total of 693 and 606 trout from the burns of Eyrland and Bu, respectively. The Eyrland sample mainly comprised trout aged 0+, 1+ and 2+ with a few aged 3+ found in 2007. The proportion of 0+ trout in the Eyrland sample ranged from 50.6% to 79.3% in the three sample years. The Bu sample comprised trout aged 0+ and 1+.The proportion of 0+ trout in the sample here was high and ranged from 71.2% to 96.2%. The Hoy burns yielded fewer trout with total samples of 354 and 269 from Ore and Whaness, respectively. The Ore sample comprised trout of all ages between 0+ and 3+, with a few aged 4+ and 5+ sampled in 2008. The Whaness sample contained trout aged between 0+ and 3+ in 2007 and 2008, although no 3+ trout were found in 2009. The proportion of 0+ trout in each burn was lower relative to the two mainland burns and ranged from 45.4% to 57.5% in Ore, and from 40.8% to 63.3% in Whaness. In each burn, there were a number of trout whose age could not be determined as scale reading was inconclusive. Length frequency graphs for each sample are shown in Figure 4.3.

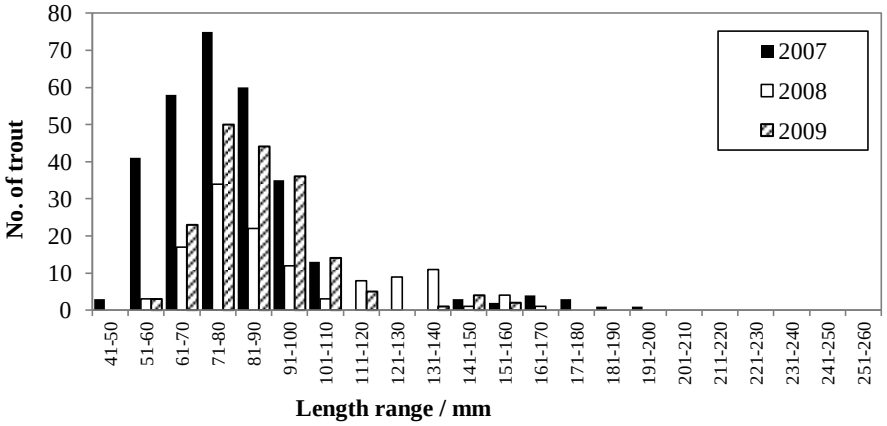
Table 4.2: Annual survey dates and sampling effort in the burns of Eyrland, Bu, Ore and Whaness, 2007 – 2009. The length and width of burn covered during each timed period was measured to calculate the total wet area fished.

Burn	Year	Dates of survey	No. of Sites	Total fishing duration (mins)	Total length fished (m)	Total wet area fished (m^2)
Eyrland	2007	7th - 13th October	7	70	272	472.9
	2008	15th - 18th October	9	93	351	779.7
	2009	2nd October	9	87	290	692.3
Bu	2007	6th - 7th October	5	50	145	168.3
	2008	22nd October	5	71	326	511.0
	2009	9th October	5	58	140	198.6
Ore	2007	29th September	6	60	223	377.3
	2008	17th October	6	91	318	530.7
	2009	9th November	6	100	336	668.6
Whaness	2007	30th September	4	40	150	308.9
	2008	11th October	4	47	190	407.7
	2009	10th November	4	54	144	312.5

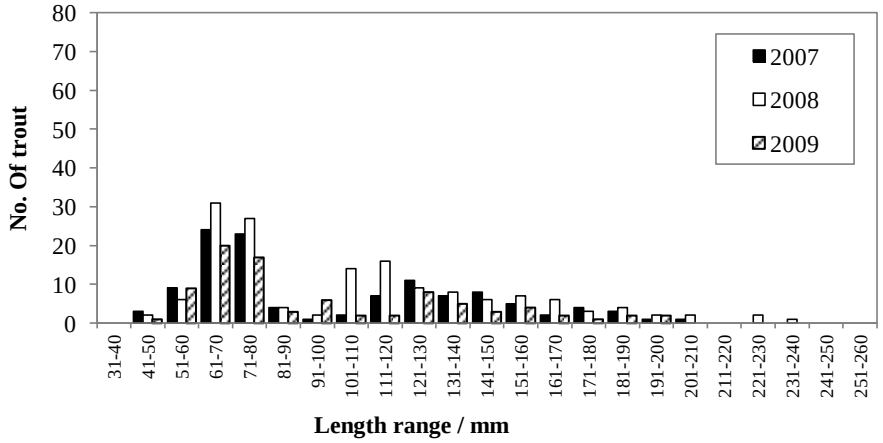
Eyrland



Bu



Ore



Whaness

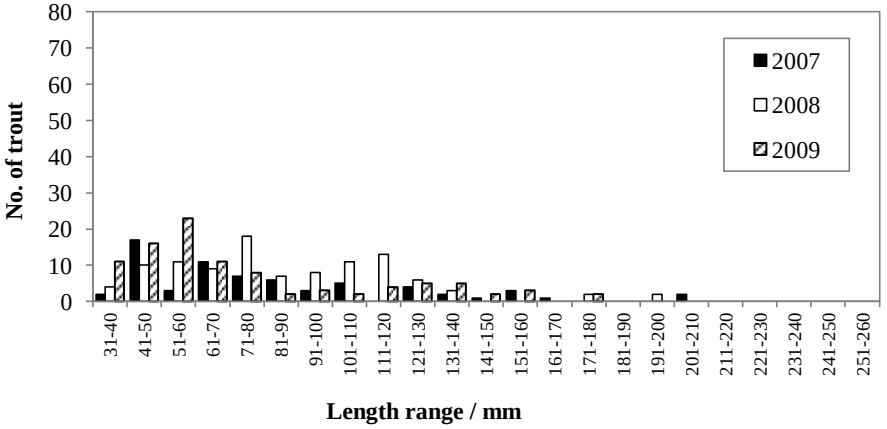


Figure 4.3: Length frequency distribution for the combined annual catch (all sample sites) of trout from the burns of Eyrland, Bu, Ore and Whaness, 2007 - 2009.

Table 4.3: Annual sample of trout from the burns of Eyrland, Bu, Ore and Whaness, 2007 – 2009. Data are total abundances by age-class combined from all sites sampled in each burn. Unclassified fish were either not aged due to lack of scales (Ore & Whaness 2007) or did not give a conclusive age from scale reading.

Burn	Year	No. trout	Number in each age cohort (% of total sample)						
			0+	1+	2+	3+	4+	5+	Unclassified
Eyrland	2007	279	183 (65.6)	80 (28.7)	14 (5.0)	2 (0.7)	-	-	0
	2008	235	119 (50.6)	104 (44.2)	12 (5.1)	0	-	-	0
	2009	179	142 (79.3)	22 (12.3)	14 (7.8)	0	-	-	1
Bu	2007	299	285 (95.3)	11	-	-	-	-	3
	2008	125	89	34	-	-	-	-	2
	2009	182	175	7	-	-	-	-	0
Ore	2007	115	63 (54.8)	-	-	-	-	-	52
	2008	152	69 (45.4)	40 (26.3)	6 (3.9)	8 (5.3)	1	1	27
	2009	87	50 (57.5)	19 (21.8)	12 (13.8)	5 (5.7)	-	-	1
Whaness	2007	68	37 (54.4)	nd	nd	nd	nd	nd	31
	2008	103	42 (40.8)	24 (23.3)	11 (10.7)	4 (3.9)	-	-	23
	2009	98	62 (63.3)	16 (16.3)	12 (12.2)	-	-	-	8

4.3.1 Growth

Table 4.4 shows the comparison of FL data for each burn in each sample year. There was no significant difference between years in the length of the main age cohorts (0+, 1+, 2+) in the burns of Eyrland, Ore and Whaness. However, significant differences occurred in the FL data for 0+ and 1+ trout from the Bu between sample years. MFL for each age cohort in each burn (pooled over the sampling period) is shown in Figure 4.4. A direct comparison of the main age cohorts (0+, 1+ & 2+) present in each burn is shown in Figure 4.5. One way ANOVA showed that the MFL of each of the three main age cohorts was significantly different in each burn (0+, $F(3, 1213) = 110.75$, $p < 0.001$; 1+, $F(3,265) = 26.19$, $p < 0.001$; 2+, $F(2, 69) = 26.91$, $p < 0.001$). Note that no fish aged 2+ from the Bu were included in this analysis. Some trout sampled may have been aged 2+ but scale reading was inconclusive.

In some cases, MFL declined with upstream distance. Figures 4.6 and 4.7 show the relationship between upstream distance and MFL in 0+ trout and 1+ trout, respectively. Regression analysis indicated that the relationship between MFL and upstream distance was significant in the burns of Eyrland, Ore and Whaness, but not in the Bu. Among 1+ trout a similar relationship was present in Eyrland and Ore populations only (Table 4.5).

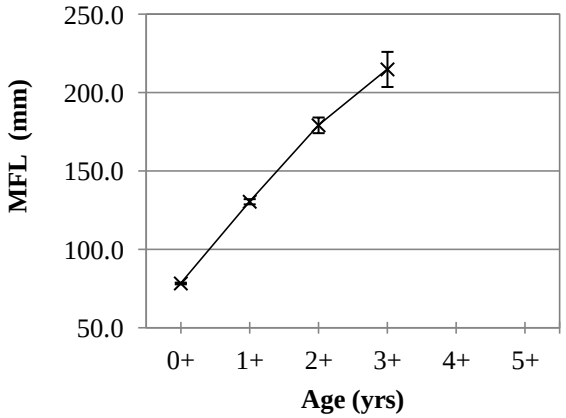
Table 4.4: Comparison of fork length between sample years of the main age cohorts of trout found in the burns of Eyrland, Bu, Ore and Whaness. In the burns of Eyrland and Bu, FL data were compared between years 2007, 2008 and 2009. However in the burns of Ore and Whaness comparisons were only possible between years 2008 and 2009 as in 2007 insufficient scale samples for age analysis were collected. Age cohorts which exhibited significant size differences between years are indicated by "".*

Burn	**Age cohort**	**ANOVA result**
Eyrland (2007 – 2009)	0+ 1+ 2+	$F(2,89) = 0.508$, $p = 0.602$ $F(2,115) = 1.863$, $p = 0.160$ $F(2,26) = 0.097$, $p = 0.908$
Bu (2007 – 2009)	0+* 1+*	$F(2,48) = 3.87$, $p = 0.022$ (2008 > 2009) $F(2,50) = 23.073$, $p < 0.001$ (2007 > 2008, 2009)
Ore (2008 – 2009)	0+ 1+ 2+ 3+	$F(2,179) = 0.155$, $p = 0.857$ $F(1, 56) = 1.840$, $p = 0.946$ $F(1, 17) = 1.116$, $p = 0.305$ $F(1, 11) = 2.075$, $p = 0.610$
Whaness (2008 – 2009)	0+ 1+ 2+	$F(2, 137) = 2.254$, $p = 0.109$ $F(1, 33) = 1.086$, $p = 0.305$ $F(1, 16) = 1.900$, $p = 0.874$

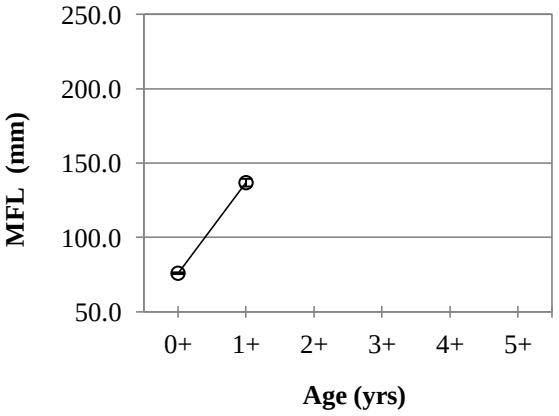
Table 4.5: Regression analysis of the relationship between MFL at each site and upstream distance (km) within the burns of Eyrland, Bu, Ore and Whaness, 2007 – 2009.

Burn	**0+**	**1+**
Eyrland	df = 9, R^2 = 78.1%, p = 0.002	df = 9, R^2 = 71.4%, p = 0.004
Bu	df = 4, R^2 = 24.6%, p = 0.395	df = 4, R^2 = 19.1%, p = 0.462
Ore	df = 5, R^2 = 71.8%, p = 0.033	df = 5, R^2 = 87.4%, p = 0.006
Whaness	df = 3, R^2 = 97.0%, p = 0.015	df = 9, R^2 = 88.3%, p = 0.060

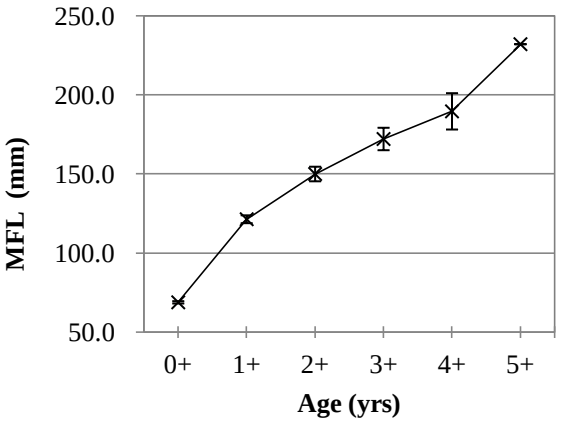
Eyrland



Bu



Ore



Whaness

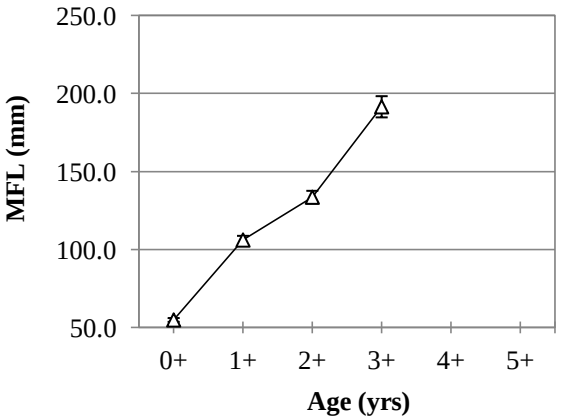


Figure 4.4: MFL (± se) of trout in each age cohort sampled from the burns of Eyrland, Bu, Ore and Whaness, 2007 - 2009. MFL was calculated using pooled data for each age cohort across the sampling period.

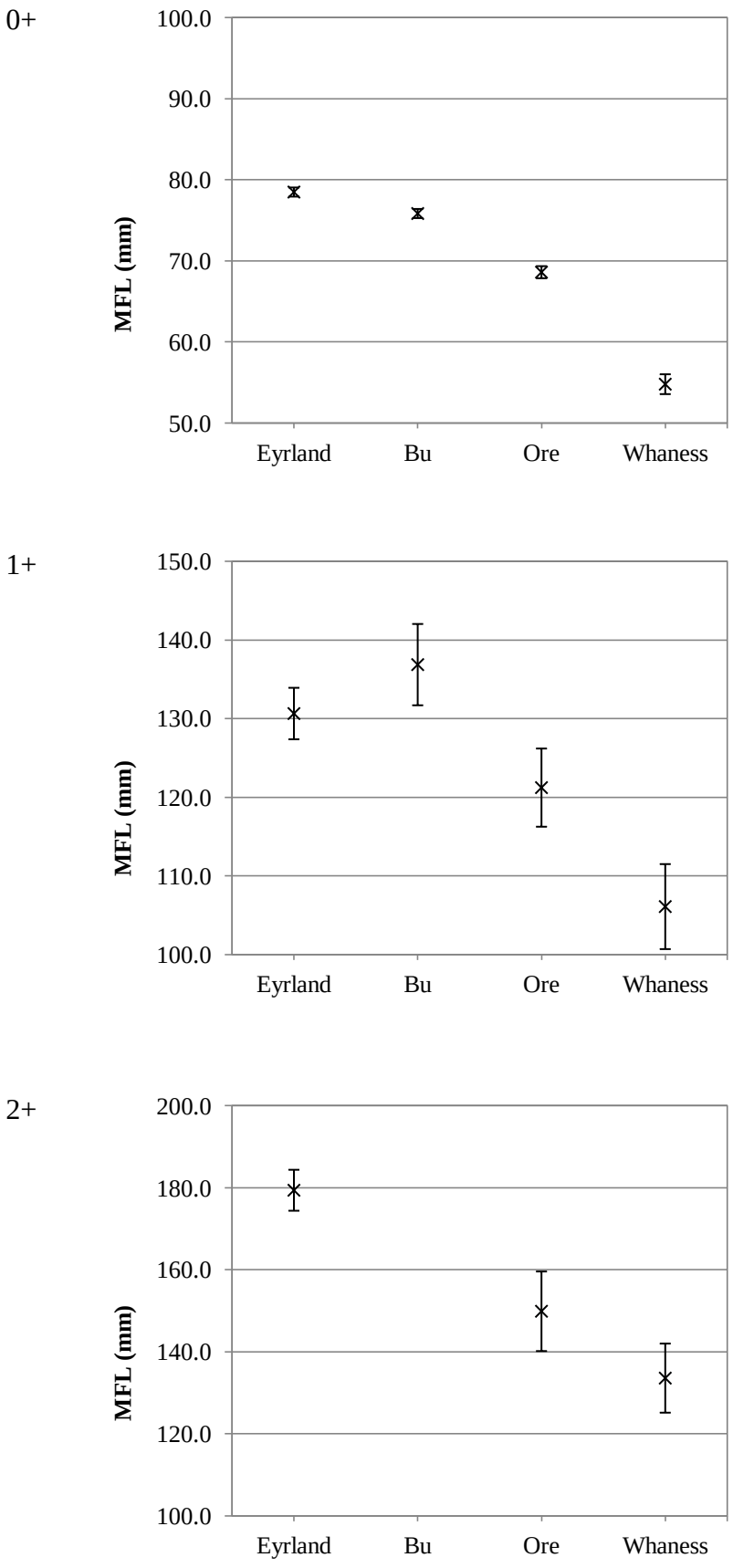
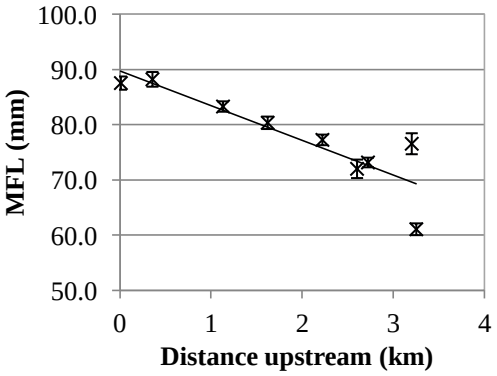


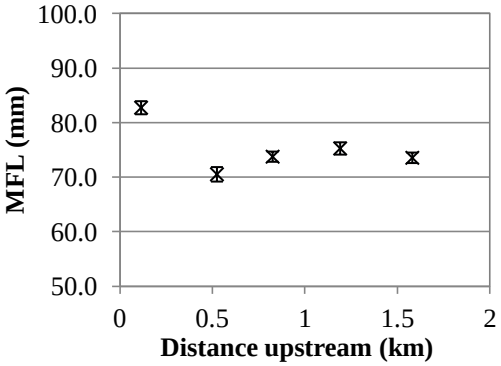
Figure 4.5: MFL (±se) for 0+, 1+ and 2+ trout sampled from the burns of Eyrland, Bu, Ore and Whaness, 2007 - 2009. MFL was calculated using pooled data for each age cohort across the sampling period.

Eyrland

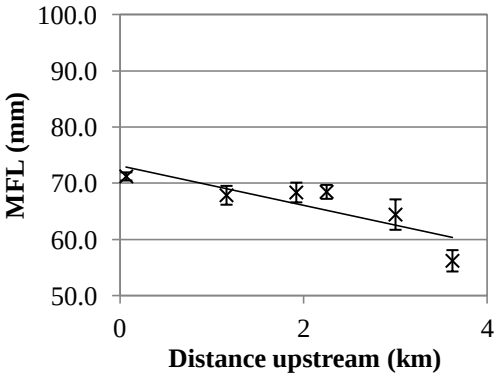


$R^2 = 78.1\%, p < 0.05$

Bu

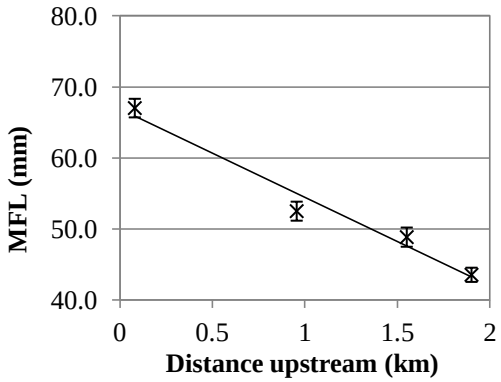


Ore



$R^2 = 71.8\%, p < 0.05$

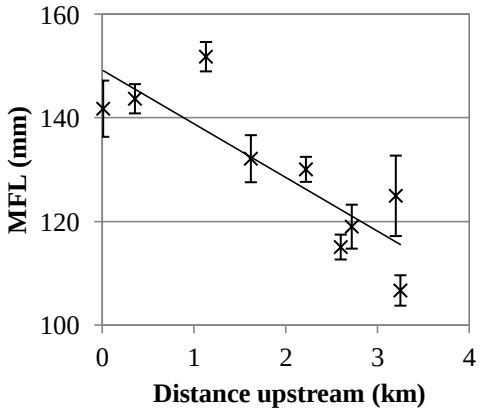
Whaness



$R^2 = 97.0\%, p < 0.05$

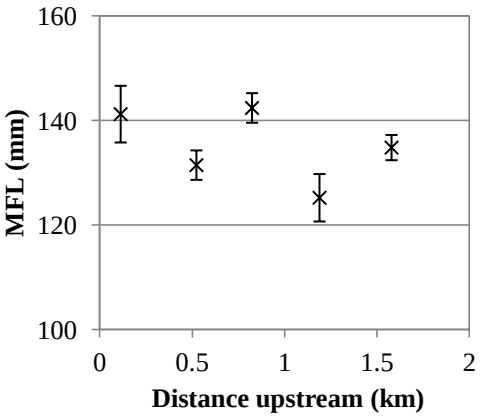
Figure 4.6: Regression analysis of the relationship between MFL ±se (mm) of 0+ trout and upstream distance in the burns of Eyrland, Bu, Ore and Whaness, 2007 – 2009. MFL was calculated using pooled data across the sampling period. Significant relationships indicated where present.

Eyrland

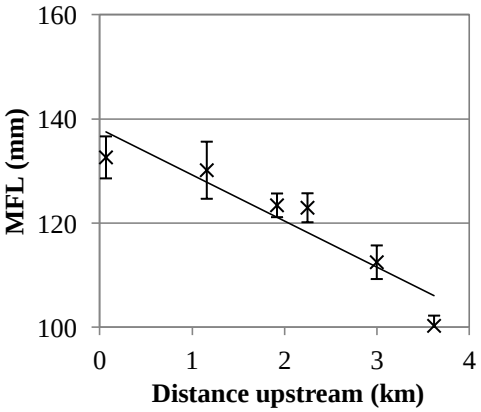


$R^2 = 71.4\%, p < 0.05$

Bu



Ore



$R^2 = 87.4\%, p < 0.05$

Whaness

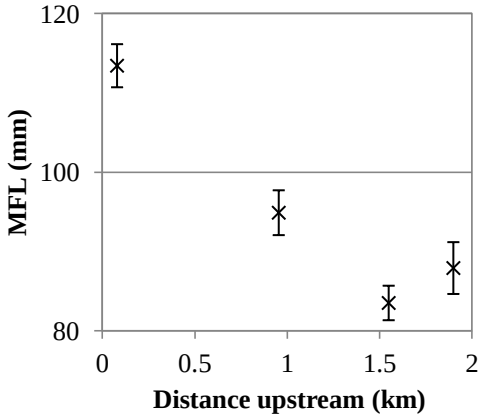


Figure 4.7: Regression analysis of the relationship between MFL ±se (mm) of 1+ trout and upstream distance in the burns of Eyrland, Bu, Ore and Whaness, 2007 – 2009. MFL was calculated using pooled data across the sampling period. Significant relationships indicated where present.

4.3.2 Trout density

Trout density (all ages) in each burn, expressed as trout caught per minute electrofishing, is shown in Table 4.6 and Figure 4.8. The highest density was recorded from the Bu in 2007 where the average trout density for all sample sites was 6.0 trout/min. In 2008 and 2009, trout density was comparable to that recorded from the Eyrland burn, which varied between 2.1 – 4.0 trout/min. In comparison, trout density in the Hoy burns was lower. In the Ore burn, density decreased over the three sample years from 1.9 to 0.9 trout/min, while in the Whaness burn, trout density showed no trend and varied between 1.7 and 2.2 trout/m. Table 4.6 also shows trout density expressed as trout caught per unit area (trout/100m^2) to enable comparison to the scoring system developed for use in the Scottish FCS (Godfrey, 2005).

Table 4.6: Trout density estimated by single run (timed) electrofishing surveys carried out in the burns of Eyrland, Bu, Ore and Whaness, 2007 – 2009. The result for each burn was calculated by averaging the trout density (catch per unit time and per unit area) at each site sampled in each year. Density is provided for all fishes aged 0+, 1++ (i.e. fishes aged 1+ or older) and all ages. The accompanying letters (A-E) represent the trout density score according to the Scottish Fisheries Classification Scheme, with A being the highest score (after Godfrey, 2005).

Burn	Year	Total no. trout	All ages (trout min^{-1})	0+ (100m^{-2})	1++ (100m^{-2})	All ages (100m^{-2})
Eyrland	2007	279	4.0	37.09 B	19.50 A	56.6
	2008	235	2.5	15.83 C	16.36 A	32.2
	2009	179	2.1	24.75 B	5.33 C	30.1
Bu	2007	299	6.0	178.64 A	6.93 C	185.6
	2008	125	1.8	21.93 C	7.73 C	29.7
	2009	182	3.1	102.10 A	3.35 E	105.4
Ore	2007	115	1.9	14.61 C	15.02 B	29.6
	2008	152	1.7	11.74 C	16.02 A	27.8
	2009	87	0.9	7.96 D	7.37 C	15.3
Whaness	2007	68	1.7	12.81 C	13.71 B	26.5
	2008	103	2.2	9.99 D	15.44 A	25.4
	2009	98	1.8	20.39 C	10.95 B	31.3

Table 4.7: Examination using two-way ANOVA (no replication) of the influence of year and site as factors in determining trout density (trout/min) within the burns of Eyrland, Bu, Ore and Whaness sampled between 2007-2009.

Burn	Year	Site
Eyrland	$F(2,12) = 14.84$, $p < 0.001$	$F(6,12) = 9.57$, $p < 0.001$
Bu	$F(2,8) = 12.53$, $p < 0.05$	$F(4,8) = 4.69$, $p < 0.05$
Ore	$F(2,10) = 3.09$, $p > 0.05$	$F(5,10) = 5.81$, $p < 0.05$
Whaness	$F(2,6) = 1.06$, $p > 0.05$	$F(3,6) = 1.51$, $p > 0.05$

Trout density measured at each site within each burn is shown for each sample year in Figure 4.9. Two-way ANOVA (Table 4.7) showed that sample year and site were significant factors in determining mean trout density in some cases. Year was significant in the two mainland burns but not in the two Hoy burns while site was a significant factor in all burns apart from Whaness in Hoy. In general, mean density was greater in downstream sites relative to upstream sites. In three of the four populations, the highest individual density was recorded at the furthest downstream site close to the tidal limit. However, regression analysis showed that in each population, the relationship between mean trout density and upstream distance was not significant (Eyrland: df = 8, R = 0.480, p = 0.191; Bu: df = 0.776, p = 0.123; Ore: df = 5, R = 0.696, p = 0.125; Whaness: df = 4, R = 0.823, p = 0.177).

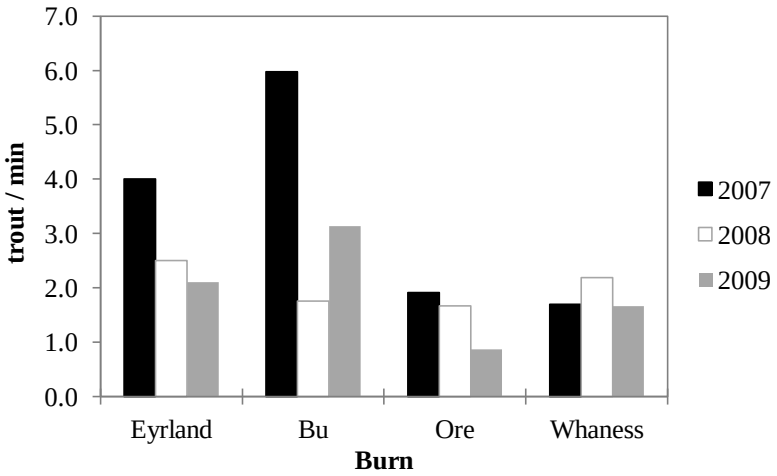


Figure 4.8: Trout density estimated by single run (timed) electrofishing surveys carried out in the burns of Eyrland, Bu, Ore and Whaness, 2007 – 2009. The result for each burn was calculated by averaging the trout density from each site sampled in each year, expressed as catch per unit time (trout/min). .

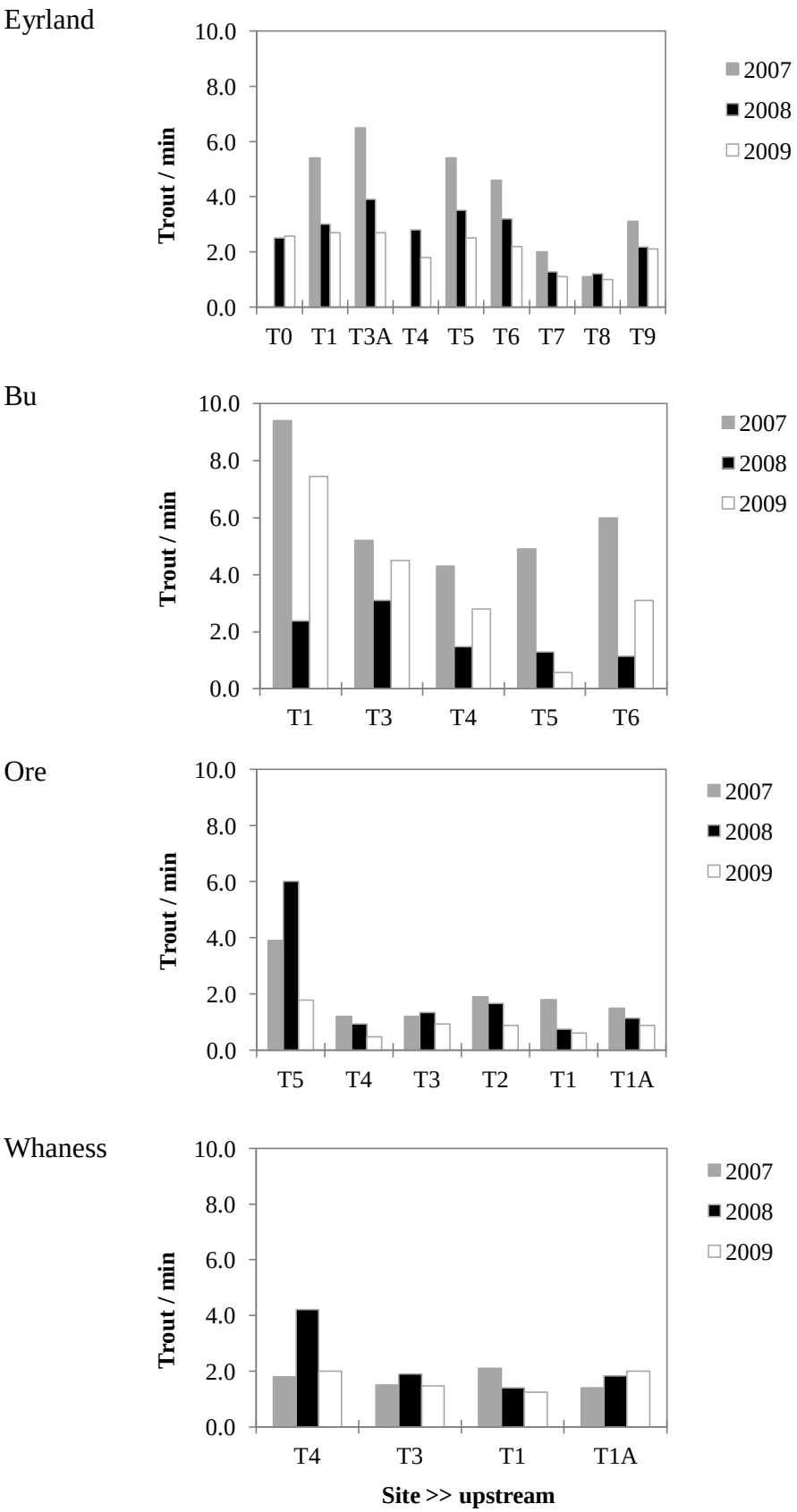


Figure 4.9: Annual trout density, expressed as catch per unit time (trout/min), at individual sample sites estimated by single run (timed) electrofishing surveys carried out in the burns of Eyrland, Bu, Ore and Whaness, 2007 – 2009.

4.3.3 Effect of density, water temperature and stream size on growth

In general, there was no correlation between MFL of 0+ trout and mean density (trout/min, all ages) between sites in each burn. The only exception to this was in the Eyrland burn in 2008 when a direct correlation was measured between the two variables among the sample sites. Results of regression analysis are shown in Table 4.8. Similarly, there was no apparent relationship between growth rate and stream size, expressed as either annual discharge or catchment area.

Table 4.8: Regression analysis of relationship between MFL (mm) of 0+ trout and trout density (trout/min) at each sample site in each sample year in the burns of Eyrland, Bu, Ore and Whaness.

Burn	Year	Regression result
Eyrland	2007	df = 7, R = 0.277, p = 0.548
	2008	df = 7, R = 0.763, p = 0.046
	2009	df = 7, R = 0.615, p = 0.142
Bu	2007	df = 5, R = 0.776, p = 0.122
	2008	df = 5, R = 0.587, p = 0.298
	2009	df = 5, R = 0.274, p = 0.655
Ore	2007	df = 6, R = 0.229, p = 0.662
	2008	df = 6, R = 0.676, p = 0.140
	2009	df = 6, R = 0.349, p = 0.497
Whaness	2007	df = 4, R = 0.216, p = 0.784
	2008	df = 4, R = 0.935, p = 0.066
	2009	df = 4, R = 0.170, p = 0.830

Mean monthly water temperature for each of the four burns is shown in Figure 4.10 and Table 4.9. Average annual water temperature was highest in two mainland burns. While average annual temperature was slightly higher in the Bu (8.8°C), average summer temperature was higher in the Eyrland burn (11.3°C). The Whaness burn exhibited the lowest annual water temperature (7.7°C). During winter, the Eyrland burn as well as the two Hoy burns had a similar average temperature (4.8 – 4.9°C) while the Bu showed a markedly higher result (5.7°C). Raw water temperature data for each burn are provided electronically in Appendix L.

Table 4.9: Average annual, summer and winter water temperatures at the burns of Eyrland, Bu, Ore and Whaness recorded between 2006 and 2010.

Burn	Average water temp. ±se (°C)	Average summer temp (April to October, °C)	Average winter temp (Nov. to March, °C)
Eyrland	8.6 ± 1.1	11.3	4.8
Bu	8.8 ± 0.9	11.1	5.7
Ore	8.3 ± 1.0	10.8	4.8
Whaness	7.7 ± 0.8	9.3	4.9

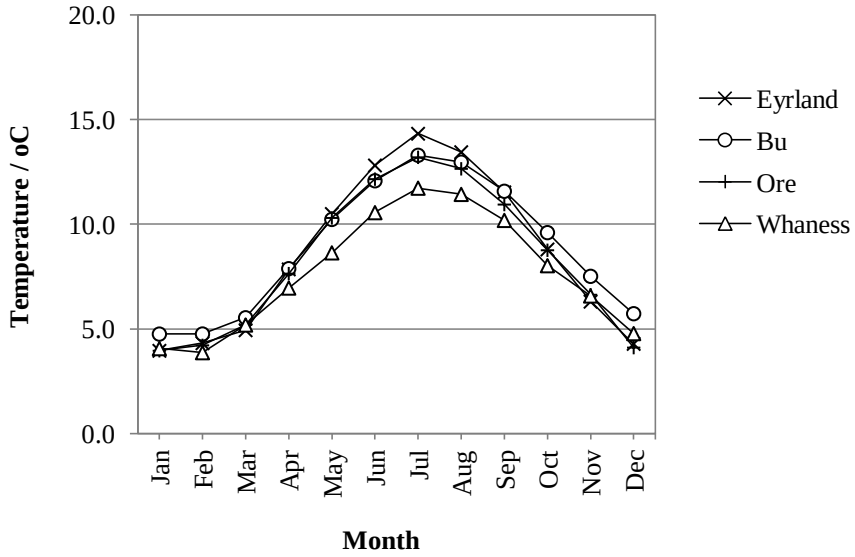


Figure 4.10: Mean monthly water temperature recorded for the burns of Eyrland, Bu, Ore and Whaness, 2006 – 2011. Water temperature data was recorded using Gemini Data Loggers (TinyTag Plus) installed at sites in the lower reaches of each burn just upstream of the tidal limit.

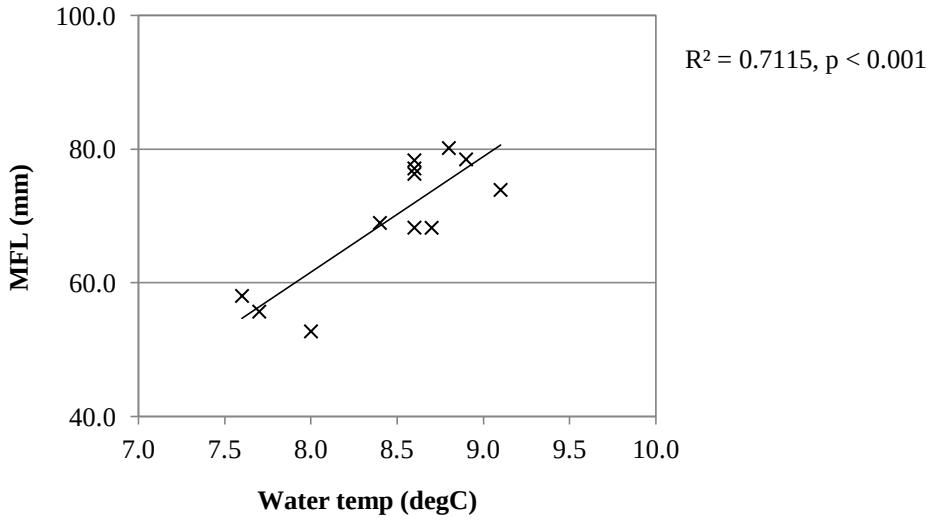


Figure 4.11: Relationship between MFL of 0+ and mean annual water temperature in each burn (n = 4) and each sample year (N = 3).

The relationship between water temperature and growth of 0+ trout in each burn and each sample year is shown in Figure 4.11. Regression analysis showed that water temperature had a significant direct effect on growth of 0+ trout ($df = 11$, $R = 0.844$, $p < 0.001$), explaining 71.2% of the variation in growth.

4.3.4 Mature resident trout

A total of 164 mature resident trout were sampled from all four burns over the sampling period, of which 148 (90%) were male (Table 9). Among the mature trout found in each burn, the percentage of males ranged from 78% (Ore) to 100% (Whaness). As part of the total sample in each burn, mature males represented between 3.1% (Bu) and 16.7% (Ore). Fewer mature female trout were found. The highest incidence of females was found in the Ore burn, where they represented 22% of the mature trout and 3.7% of the total population. No mature female residents were found in the Whaness burn.

The MFL of different aged mature male parr in each burn is shown in Figure 4.. MFL of mature male trout from the burns of Eyrland, Ore and Whaness ranged from 161.8mm to 167.4mm, while male trout found in the Bu were 133.3mm long on average. One-way ANOVA followed by post hoc test showed that males were significantly smaller in the Bu compared to the other three burns ($F(3,165) = 5.17$, $p< 0.05$). The smallest mature males found in each burn varied from 109mm (Eyrland) to 119mm (Whaness). Male trout were youngest in the mainland burns with an average age of 1.4 (± 0.06) years and 1.0 (± 0.0) years in the Eyrland and Bu burns, respectively. Average age in the Ore and Whaness burns was 2.5 (± 0.24) and 2.4 (± 0.15) years, respectively. The average size of female residents varied from 140mm (Bu) to 245mm (Eyrland). The smallest female was 135mm and was sampled from the Bu. Mean age varied from 1.0 years to 2.7 years in the Bu and Ore burns, respectively.

MFL for different aged male trout in each population is shown in Figure 4.12. Growth rate did not appear to directly influence either the incidence of mature resident males across the four populations. Mature males were most frequent and largest in the Ore burn, where growth in freshwater was relatively slow. Mean size of male residents was greatest in the Ore burn largely due to the presence of older, larger trout. One-way ANOVA showed that resident males aged 1+ and 2+ were significantly larger in the Eyrland population compared to same aged males in the other burns (1+, $F(2,60) = 5.89$,

Table 4.9: Total number, size and age of mature resident trout sampled from the burns of Eyrland, Bu, Ore and Whaness, 2007 – 2009.

Burn	Sample	No. mature trout	Male					Female				
			No. (%)	Age (yrs)	MFL ±se (mm)	Range (mm)	Mean age ± se (yrs)	No. (%)	Age (yrs)	MFL ±se (mm)	Range (mm)	Mean age ± se (yrs)
Eyrland	693	74	71 (10.2)	1, 2, 3	162.8 ± 3.2	109 – 225	1.4 ± 0.06	3 (0.4)	2,3	225.7 ± 9.9	212 – 245	2.3 ± 0.33
Bu	606	19	17 (2.8)	1	133.3 ± 36	112 – 157	1.0 ± 0.00	2 (0.3)	1	140.0 ± nd	135 – 145	1.0 ± 0.00
Ore	354	59	46 (13.0)	1,2,3,4,5	167.4 ± 41	112 – 232	2.5 ± 0.24	13 (3.7)	2,3,4	166.6 ± 5.4	140 – 200	2.7 ± 0.29
Whaness	269	14	14 (5.2)	2,3	161.8 ± 8.3	119 – 205	2.4 ± 0.15	0 (0)	-	-	-	-

$p < 0.05$; 2+, $F(2,24) = 14.90$, $p < 0.001$). Regression analysis (Figure 4.13) also showed that the frequency of mature males in each population was directly related to stream size (as catchment size, df = 3, R = 0.953, p = 0.047. However, the relationship between stream size and MFL of mature male residents was not significant (df = 3, R = 0.862, p = 0.138). In addition, the relationship between populations growth rate, expressed as mean annual growth increment, and mean male age was not significant (df = 3, R = 0.937, p > 0.063).

Mature female residents were much less abundant that male trout in each population and none were found in the Whaness burn over the entire sampling period. Mature females were most common in the Ore burn, where they represented 3.7% of the total sample. The incidence of mature female residents in each population was not related to stream size (df = 3, R = 0.545, p > 0.455). Similarly, there was no relationship between female MFL and stream size (df = 2, R = 0.787, p = 0.423) or between mean population growth rate and mean age of mature females in each populations (df = 2, R = 0.978, p = 0.134). The frequency of males and females combined was not directly related to catchment size (df = 3, R = 0.883, p = 0.117).

4.3.5 Growth in mature and immature trout

MFL for each age cohort of mature male and female residents, along with immature parr, is shown in Figure 4.14. In general, mature males were larger than same aged immature trout. However, analysis using one-way ANOVA showed that this difference was only significant in the Eyrland burn, for trout aged 1+ (Table 4.10). In the Bu, mature males of age 1+ were slightly smaller on average than same aged immature trout, although the difference was not significant. A similar comparison in mature female residents was only possible in trout aged 2+ from the Ore burn, where mature female trout were significantly larger than same aged immature parr. There were insufficient females to statistically compare their size to same aged mature male trout.

Table 4.10: Comparison (one-way ANOVA) of FL between same aged mature, female and immature parr in the burns of Eyrland, Bu, Ore and Whaness, 2007 – 2009.

Gender	Burn	Age cohort (yrs)	MFL (mm)		ANOVA result
			Immature	Mature	
Male	Eyrland	1+	126.8	143.4	$F(1,190) = 36.53$, $p < 0.05$
		2+	177.6	186.7	$F(1,36) = 3.50$, $p > 0.05$
	Bu	1+	144.6	136.9	$F(1,49) = 1.32$, $p > 0.05$
	Ore	1+	117.8	126.0	$F(1,56) = 0.93$, $p > 0.05$
		2+	143.2	158.0	$F(1,14) = 3.68$, $p > 0.05$
	Whaness	2+	130.2	141.6	$F(1,22) = 1.65$, $p > 0.05$
Female	Ore	2+	141.0	174.3	$F(1,13) = 9.53$, $p < 0.05$

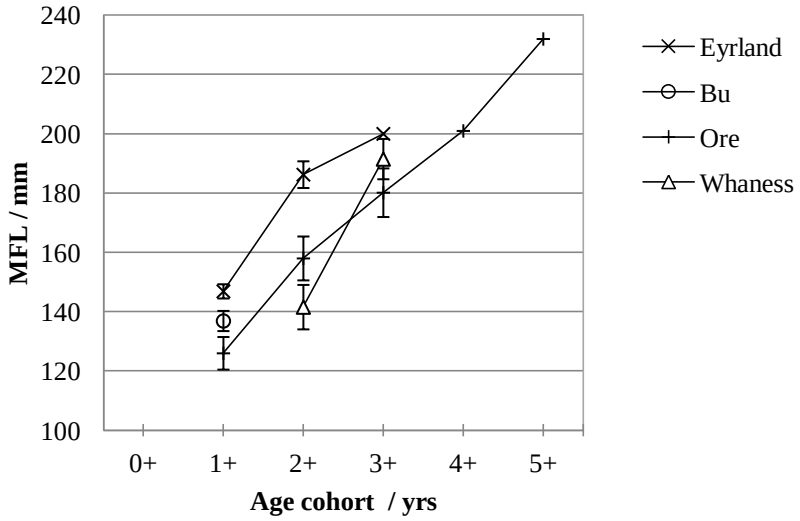


Figure 4.12: MFL ±se (mm) for each age cohort of mature male trout sampled from the burns of Eyrland (N = 69), Bu (N = ,16) Ore (N = 46) and Whaness (N = 15), 2007 – 2009.

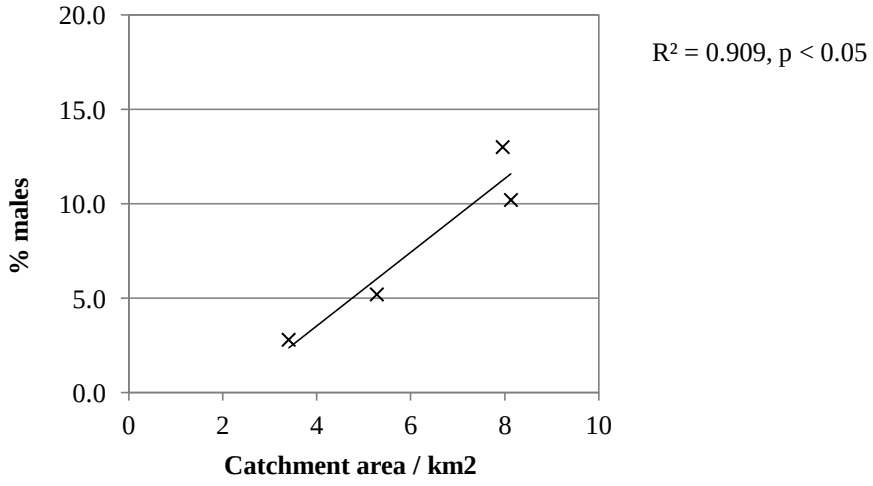
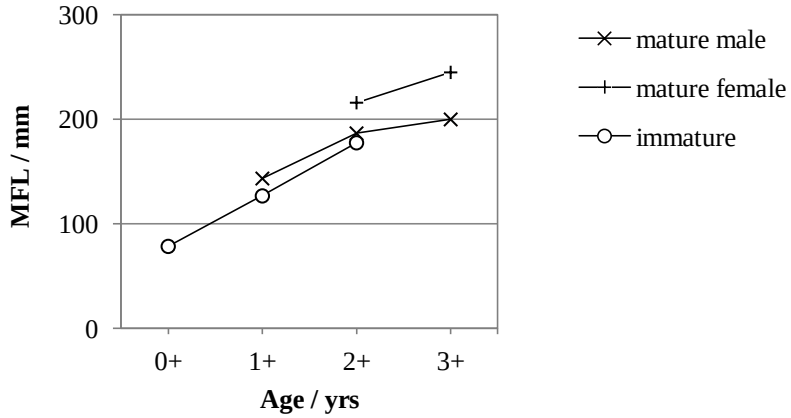
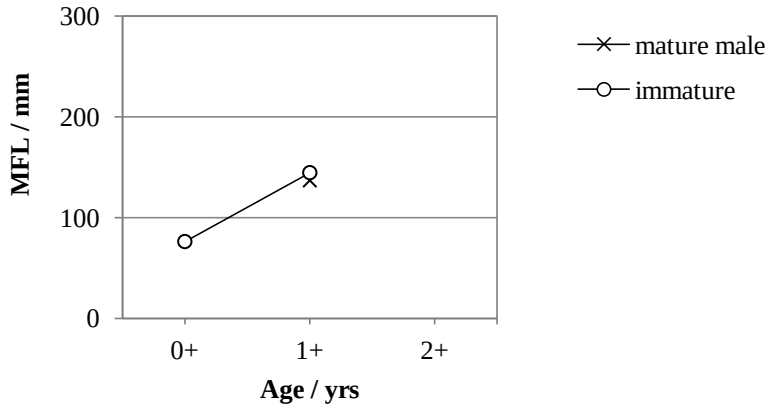


Figure 4.13: Incidence of mature male resident trout as a % of the overall sample compared to the catchment area of the burns Eyrland, Bu, Ore and Whaness.

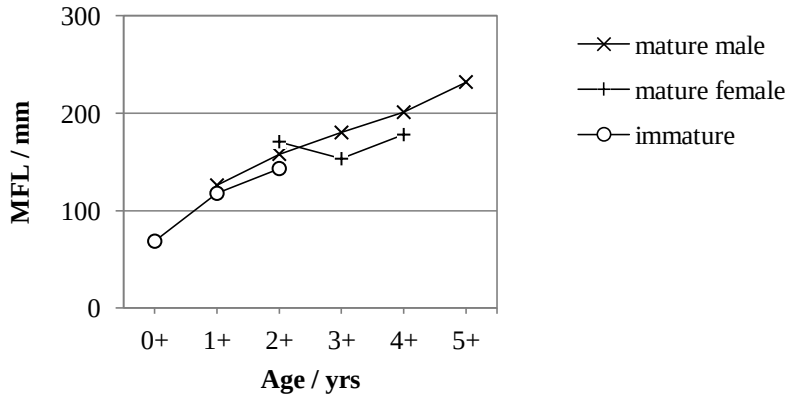
Eyrland



Bu



Ore



Whaness

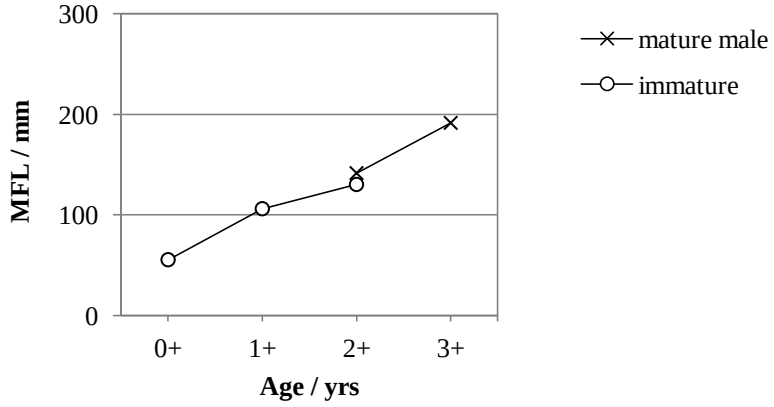


Figure 4.14: MFL for each age cohort of mature male and female resident trout along with immature parr sampled from the burns of Eyrland, Bu, Ore and Whaness, 2007 – 2009.

4.4 Discussion

The results confirmed that in general, trout in the mainland populations grew faster than trout from the Hoy populations. This difference related to both immature and mature parr. The density of trout was also lower in the Hoy populations, suggesting that it did not have a negative effect on growth. Among trout aged 0+, FL decreased with upstream distance in three of the four sample populations. Among trout aged 1+, FL decreased with upstream distance in only two populations. Despite their close proximity, mean monthly and annual water temperature varied between the four burns and this appeared to have a significant direct effect on growth in 0+ trout. Mature resident fishes were predominantly male and their incidence (as a % of the total sample in each population) was directly related to stream size (as catchment area). Mature female residents were rare apart from in the Ore burn, but their frequency and size were not related to the general growth rate or stream size between the four populations. While the average size of mature male parr was generally larger than same-aged immature parr, this difference was only significant in one comparison out of six. Mature females were significantly larger than same-aged immature parr in the one instance where this comparison was possible.

Growth of anadromous trout in freshwater is thought to have a significant influence on future migratory behaviour. For example, slow growth in nutrient poor systems is thought to encourage anadromy over residency and *vice versa* (Northcote, 1978; Gross *et al*., 1988). Between populations, faster growth also appears to result in earlier (*i.e.* younger) migration to sea (Toledo *et al*., 1993; Euzenat *et al*., 1999). Results from Chapter 3 suggested contrasting growth rates between trout populations on mainland Orkney and on the island of Hoy. The results presented here confirmed this observation and showed that the two Hoy populations were slower growing relative to trout in the mainland populations. The results also showed that in three of the four sample burns, growth of 0+ and 1+ aged trout decreased with upstream distance, as observed previously (Egglishaw & Shackley, 1977; Maisse & Bagliniere, 1991). The specific aims of this chapter however were to assess the significance of fish density, temperature and stream size as factors governing trout growth during their freshwater phase.

The density of trout varied between years and between burns. While the overall density estimates were higher in the two mainland burns, this was mainly the result of high

numbers of trout in the 0+ age cohort. The Bu in particular supported extremely high numbers of 0+ trout, comfortably within the "A" classification of the Scottish FCS for streams of <4m width (Godfrey, 2005). In contrast, the Hoy burns did not score higher than "C" for 0+ trout. This supports previous observations by Harbinson (1998) that spawning substrates in Hoy burns are limited. However, the Hoy burns scored more highly for older trout (aged 1+ or older), between "A" to "C", which was similar to scores in the Eyrland burn. In contrast, the Bu, so productive in terms of 0+ trout, supported relatively few older trout, producing scores no better than C over the three year sample period. The question therefore is where do all the 0+ trout go? Two options exist – they either die or migrate out of the burn to the sea. The tendency for small streams to produce younger smolts has been reported elsewhere (Titus & Mosegaard, 1992; Bohlin *et al.*, 2001). The anadromous behaviour of trout in the Bu and the three other populations will be examined in Chapter 5.

Trout density in both Hoy burns was greatest at the furthest downstream sites in some years. The presence of larger numbers of fry at the downstream sites could have resulted from migration from further upstream. Downstream movements of 0+ fish during their first summer is a well studied phenomenon and in salmonids and is often associated with moribund fishes or those which have been competitively excluded by larger more aggressive fry (Elliott, 1994; Skoglund & Barlaup, 2006; Johnson *et al*., 2013;). It has already been demonstrated that in each burn, the mean size of trout at the furthest downstream sites was similar or larger than those sampled from upstream sites, so competitive exclusion is an unlikely explanation for this occurrence. Suitable spawning habitat was present at both sites and newly emerged fry were caught there each year between 2007 and 2010 when the author was electrofishing for smolts. It is possible that the lower reaches of both Hoy burns represent important spawning habitat for trout, particularly if such substrates are limited further upstream (Harbinson, 1998). The occurrence of low trout density in some years was unexplained but might simply be due to variation in spawning success. Being near the tidal limit, these sites could also be exposed to increased salinity during large spring tides. This was witnessed at both sites when the salinity increased sufficiently to render electrofishing ineffective although the maximum salinity reached at the sites was unknown. Brown trout eggs may survive and hatch in salinities up to 4ppt (Landegren & Vallin, 1998). The impact of saline incursion may vary with the amount of water flow in the burn at the time and

further information is required to determine the impact of saline incursions on spawning and rearing capacity in these areas.

Did trout density or the other factors included in this study, i.e. stream size and water temperature, affect the freshwater growth rates of trout in the study populations? It was clear that high density of trout had little or no detrimental influence on mean growth either between or within each of the four populations. Mean growth between similar age cohorts was clearly higher in the two mainland burns where density was also higher. This finding agrees with other studies on brown trout (Egglishaw & Shackley, 1977; Mortensen *et al*., 1988). However, Elliott (2015) reported that while mean growth may be unaffected by density, a density dependant effect on growth can be apparent in the slowest and fastest growing trout in a cohort. It was not possible to study this effect in the present study.

In salmonids, an indirect correlation between freshwater growth rate and latitude has been reported (Jonsson & L'Abée-Lund, 1993). Of course the factor which varies broadly with latitude is temperature and this study highlighted that access to temperature data in the analysis of growth in trout populations is crucial, particularly in a local context. Here it was found that despite their close proximity, water temperature in the four burns was different, with the highest annual mean being found in the Bu and the lowest in Whaness. The reason for this temperature difference was unclear but could be linked to catchment altitude, burn aspect (*i.e.* exposure to sunshine), slope, catchment type or groundwater inputs. As well as being the warmest, the Bu exhibited the least annual variation in water temperature, where the opposite might be expected, in what was the smallest of the four burns. The Bu is known to receive groundwater inputs (J. Stevenson, pers comm.) which could explain the low variation in temperature. Consequently, it is perhaps unsurprising that a direct relationship was observed between growth and water temperature between the four burns, in common with other studies (Mortensen *et al*., 1988; Elliott, 1984).

A direct relationship between stream size and freshwater growth rate in salmonids has been reported (N. Jonsson *et al*., 1991). Few studies compare the growth rate of same aged immature trout in different sized streams. In this case, there was no significant relationship between freshwater growth rate and stream size, therefore the hypothesis was refuted.

Of the factors discussed here, only temperature appeared to have a significant effect on freshwater growth across the four populations. While it was hoped that the influence of stream size and density on growth could be assessed in isolation from temperature by choosing four burns located very close to each other, the unexpected variation in temperature between the burns made this difficult. However it does suggest that temperature is more influential than the other parameters examined here in governing freshwater growth dynamics among brown trout. The possible role of other factors not tested here should of course be considered too, such as food availability, water chemistry and habitat availability. In an analysis of invertebrate populations in several Orkney burns, Kirby (2012) found a particularly impoverished fauna in the Whaness burn which it was argued was the result of low pH, which characterizes most freshwater systems on Hoy due to its extensive peat soils (Duncan *et al*., 1992). It is possible therefore, that both low temperature and acidic water conditions could be responsible for the slow growth observed in the Whaness burn.

Among mature residents, males dominated, in common with other studies of anadromous brown trout populations (Campbell, 1977; Jonsson *et al*., 2001). The absence of mature female residents from the Whaness burn was particularly interesting, especially considering that the highest incidence of mature females was found in the neighbouring Ore burn, which otherwise exhibited similar population characteristics, *i.e.* relatively slow growth and high average age. The incidence of mature female residents between the four populations could not be explained by growth rate, density or stream size. Sampling errors or shortcomings cannot be ruled out, *e.g.* mature females may have been mis-identified as immature trout or the sample may not have been large enough to properly capture the frequency of mature females in the overall population.

It has previously been reported that between different populations, freshwater growth rate has a significant direct effect on the incidence of mature resident fishes, particularly males (L'Abée-Lund *et al.,* 1990). This supports the general concept that good growth conditions in freshwater promote maturity over migration (Gross *et al*., 1988; L'Abée-Lund *et al*., 1990; Olsson *et al*., 2006). The results obtained here do not support this hypothesis. The incidence of either mature male or female resident trout was not related to growth rate across the four populations. The incidence of both males and females was highest in the Ore burn, where growth was slow relative to the other populations. A direct relationship was detected between the frequency of mature male trout but not

female trout. Furthermore, the overall frequency of mature residents (male and females combined) was not related to catchment size or growth rate across the four populations. These results do not support the hypothesis that fast growth promotes maturity before anadromous migration reported elsewhere (see above) although the low sample size (n=4) should be noted. It would clearly have been interesting to have data on the growth and incidence of mature resident trout in all 23 of the anadromous populations identified in Chapter 3, but this was simply beyond the scope of this project. However, in terms of growth *within* populations, it is the relative growth between resident and migratory individuals which might be the more relevant influence on the decision between residency and anadromy. Dellefors & Faremo (1988) noted that within populations, the frequency of mature resident males increased in years when freshwater growth was good and *vice versa*. The same behaviour has been noted in Atlantic salmon (Myers *et al*., 1986). In this case it was possible to test the relative growth between mature residents and same-aged immature parr, where the latter group provide a proxy for trout which if they are not mature, might go on to migrate. In the seven instances where this comparison was possible (six cases of male residents versus immature parr, one case of female residents versus immature parr), there was no difference in average size in five cases. In both remaining cases, mature trout were longer in each (Eyrland 1+ males, Ore 2+ females). Clearly however, the assumption that immature parr adequately represent the anadromous fraction of each of the sample populations is unsafe and more work to better characterize anadromous individuals will be carried out in Chapters 5 & 6 so that a better comparison of growth can be made between the two groups.

Between populations, stream size (as discharge) has also been reported to have a direct influence on the mean size in mature male residents (Jonsson *et al.*, 2001). In this study, the relationship was not significant, although the relatively low sample number (n=4) should again be considered. Mature males in the Ore burn were the largest on average in the four populations. However, this result was not surprising given that the Ore burn yielded five age cohorts of mature residents in contrast, for example, to the Bu, where only one age cohort (1+) was present. If a comparison was made between same-aged males in each population, it was evident that male size followed the general growth trend evident between the four populations. For example, the mean size of males aged 1+ from each population, in decreasing order, was Eyrland Bu then Ore. Therefore, the populations with the fastest general growth rate produced faster growing

males, which was not a major surprise. It could be suggested that the lack of older mature males in the Bu reflected its small size and limited potential for supporting older, larger individuals. The natural progression from this is to hypothesize that migration is the tactic preferred over maturation in freshwater in systems of that size. This will be examined in the next chapter when characteristics of smolts migrating from each of the four systems will be examined.

In summary, the data confirmed that freshwater growth rate was slower in the Hoy populations relative to the mainland populations. MFL in trout parr decreased with upstream distance in the larger burns but not in the smallest. Trout density, stream size and water temperature did not appear to have any influence on freshwater growth rate between the four study populations. The frequency of mature male (but not female) residents was directly related to stream size. However, there was no relationship between stream size and the combined frequency of male and female residents between the four populations. Similarly, the mean size of male and female residents was not related to either stream size or growth rate. While mature residents were generally larger on average than same aged immature trout, these differences were not significant.

CHAPTER 5. GROWTH CHARACTERISTICS OF SMOLTS IN FOUR ANADROMOUS BROWN TROUT POPULATIONS.

5.1 Introduction

Populations of anadromous brown trout are characterised by a spring migration of juvenile trout, known as smolts, from freshwater to the sea (Hoar, 1988). This migration comprises individuals of different age and size. For a single year class of juveniles, some will migrate after one year in freshwater, while others may migrate after two, three or more years. In each year therefore, smolts of different ages from different year classes will migrate to sea together. The mean smolt age (MSA) in a population is largely determined by growth rate in freshwater (Jonsson & L'Abée-Lund, 1993). As temperature has a strong influence on growth rate, the MSA of a population tends to increase with latitude. While populations in Spain and France mostly smolt at age one or two, sea trout smolts up to eight years old have been recorded in northern Norway (Toledo *et al*., 1993; L'Abée-Lund *et al*., 1989). In Scotland, sea trout smolts of all ages between one and four have been recorded (Nall, 1930; Pratten & Shearer, 1983a). Within populations, smolt size tends to vary directly with age, *i.e.* older smolts are larger than younger smolts. However, older smolts aren't necessarily larger when comparing across populations. In a review of 102 European sea trout populations, including two in Orkney, mean smolt size varied from 10.7cm to 25.2cm and no relationship with latitude was evident (Jonsson & L'Abée-Lund, 1993). Other studies have reported smolts as small as 6cm in small Norwegian streams and as large as 27cm in the Owenglena and Invermore systems in Ireland (Jonsson *et al*., 2001; Gargan *et al*., 2006).

Apart from age, a number of other factors, such as freshwater growth rate and stream size, can also influence smolt size. In a study confined to Norway, smolt size increased in more northern populations, suggesting that slower growth resulted in older, larger smolts (L'Abée-Lund *et al*., 1989). This contradicts the findings of the pan-European study, noted above, where no link was found between mean smolt size and latitude. Jonsson *et al*. (2001) found that smolt size varied directly with water discharge but only in small streams up an annual mean discharge of 0.2 cumecs. Other studies also describe the migration of small (and young) smolts from small streams flowing into the

Baltic Sea (Borgstrøm & Heggenes, 1988; Titus & Mosegaard, 1989; Landergren, 2001). Whether these latter examples involve true smoltification is unclear as the salinity of the "sea" in these studies was <7ppt. Such behaviour could be a special adaptation in populations inhabiting very small streams which discharge into a low salinity marine environment, in the same way that smolt size was observed to increase in populations occurring in the coldest northern extremes of the brown trout distribution, noted earlier. The impact of stream size on smolting in sea trout has been rarely studied outside Scandinavia and its precise influence remains an area of research interest.

Smolt size, and hence the factors which influence it, is an important area of research as it has an impact on the rate of survival following migration into the marine environment. It has been clearly demonstrated that in comparison to smaller smolts, larger smolts exhibit higher survival rates in the transition to saltwater as they are able to osmoregulate more efficiently and are also less vulnerable to predators (Hoar, 1988; Dieperink *et al*., 2002). It has been proposed that salmonid smolts must reach a minimum size before migrating to sea, to improve their chances of survival for the reasons mentioned above. The so-called threshold size theory was hypothesized by Elson (1957) for Atlantic salmon and later by Fahy (1985) for anadromous brown trout. However, recent literature does not support such a mechanism and the presence of a universal threshold size has been rejected (Økland, 1993). The relatively wide range in mean smolt size reported in trout populations across Europe also undermines the hypothesis (Jonsson & L'Abée-Lund, 1993).

While there presence of a threshold size in anadromous has been refuted, Fahy's research into Irish sea trout populations represents an extensive and revealing collection of work on sea trout growth dynamics. The presence of B-type growth (or B-growth) in smolts, that is growth achieved in freshwater between the end of the last winter in freshwater and migration to sea, was noted in several populations, *e.g.* Beltra and Currane (Fahy, 1981; Fahy & Rudd, 1988). It was this last minute but significant increase in size among some smolts that was used as evidence of a threshold size (Fahy, 1985). This was evidently insufficient to prove the presence of a universal threshold size but nevertheless, supported other work which demonstrated the importance of size and survival at sea. It is surprising therefore that the subject of B-growth has rarely appeared in the literature since then. Pratten & Shearer (1983a) noted the occurrence of

B-growth (they termed it "plus" growth) in smolts migrating from the River North Esk in Scotland. Caballero *et al*. (2006) also noted the presence of B-type smolts (*i.e.* those which exhibited B-growth) in a Spanish population but neither study quantified the extent of B-growth or its contribution to smolt size at migration. The possibility that B-growth could have a significant influence on size, and that size influences survival at sea, is ample justification for more detailed research on this subject, *e.g.* are the dynamics of B-growth predictable or random?

The current literature provide wide ranging, contrasting but rather basic information on size and growth patterns in smolting trout. The impact of stream size and freshwater growth rate on subsequent smolt size remains unclear. Literature on B-growth suggests that in some populations at least, there is a last-minute surge in growth prior to entering the sea. The dynamics of B-growth and its presence in other populations is poorly understood. Therefore, the specific research questions set in this chapter were:

- What are the size and age characteristics of smolts produced by each of the four populations;
- Does freshwater growth rate have an impact on smolt size and/or age;
- Does stream size have an impact on smolt size and/or age;
- What is the magnitude of B-growth expressed by smolts in each population; and
- Is B-growth random or is it dependant on previous growth performance.

These questions were considered by expanding on the previous chapter in an examination of anadromous brown trout smolts produced from the burns of Eyrland, Bu, Ore and Whaness in Orkney.

5.2 Methods

The reader is referred to Chapter 2 for detailed information on the Orkney area and methods. A summary of the study sites and methods used in this chapter are provided below.

5.2.1 Study sites

Brown trout smolts were sampled from four burns which all drain into Scapa Flow. The burns of Eyrland and Bu were located on the Orkney Mainland while the burns of Ore and Whaness were located on the island of Hoy, to the west of Scapa Flow. The burn mouths are within 11km of each other. Locations and catchment details have already been provided in Chapter 4 (Table 4.1).

5.2.2 Smolt sampling

Each spring between 2007 and 2010 inclusive, smolts were sampled from each of the four burns. In the Eyrland burn, smolts were captured using an inclined plane fish trap, situated approximately 100m upstream of the tidal limit. In the burns of Bu, Ore and Whaness, smolts were sampled by single pass electrofishing surveys in the lower reaches of each burn, starting approximately at the tidal limit and working upstream. In each year, Surveys were carried out approximately at weekly intervals through the spring period, depending on water level. Full details of trapping and electrofishing methodologies are provided in Chapter 2. It was assumed that all smolts caught in the fish trap or by electrofishing were on the verge of seawater entry, given the proximity of sampling sites to the sea.

5.2.3 Fish processing

All smolts were processed according to the methods for fish processing found in Chapter 2.

5.2.4 Scale reading

Scale reading was carried out according to the method described in Chapter 2.

5.2.5 Length nomenclature

The terms cMFL and oMFL relate to smolt size at the end of the last winter annulus in freshwater and at the moment of sampling, respectively. These terms and the methods used in their estimation are described fully in Chapter 2. Furthermore, for the purposes of the discussion, the moment of sampling was assumed to equate to the moment of seawater entry.

5.2.6 Data analysis

Data analysis was carried out using SPSS, versions 14 and 16. Comparison of fork length data was carried out using ANOVA. A p-value of 0.05 was used unless stated otherwise. Where more than two groups were being compared a post-hoc test (Fisher's LSD) was used to identify significant differences between the mean values of individual groups. Regression analysis was carried out using Microsoft Excel.

5.3 Results

Smolts were sampled successfully from each of the four burns. Over the four sample years, the trap in the Eyrland burn provided a total sample of 1896 smolts, while electrofishing in the burns of Bu, Ore and Whaness electrofishing yielded totals of 216, 239 and 182 smolts, respectively. Smolts comprised individuals of all ages between one and four years and ranged in FL from 101mm to 233mm. A summary of the catch from each burn in each year is provided in Table 5.1. Length frequency distributions of smolts sampled from each burn in each year are shown in Figure 5.1. The raw data from each year's trapping and electrofishing carried out in each burn are contained in Appendices M to P.

5.3.1 Age and size

MSA was younger among smolts from the mainland burns compared to those from the Hoy burns. S2 smolts dominated the sample from the Eyrland burn, accompanied by smaller numbers of S1 and S3 smolts. MSA of all smolts over the four year sample period was 2.0 years. In the Bu, both S1 and S2 smolts were abundant with one or the other dominating in each year. Here, MSA was 1.5 years over the four sample years. In the Hoy burns, one year old smolts were almost entirely absent, with only two individuals being found in total over the four sample years. In the Ore burn, S2 smolts dominated along with smaller numbers of S3s, with an overall MSA of 2.2 years. In the Whaness burn, S3 smolts were most prevalent in each year, followed by S2s and a small number of S4s in each year, resulting in a MSA of 2.6 years. In summary, S1 and S2 smolts were prevalent in the two mainland burns while S2 and S3 smolts were dominant in the two Hoy burns.

The oMFL (all burns, all ages) over the sampling period was 160.1 ± 0.4mm (N=2531). The largest oMFL (all ages) was found in the Eyrland population (163.1 ± 0.7mm), despite the fact that the MSA here was smaller than that in the two Hoy populations. The smallest oMFL was found in the Bu (144.9 ± 1.2mm). The average smolt size in each population and in each sample year is illustrated in Figure 5.2. While this suggests some broad trends, the comparison of oMFL between populations was complicated by variation in the relative abundance of each age cohort between the four populations, as described above. To overcome this problem, the size of same-aged smolts was

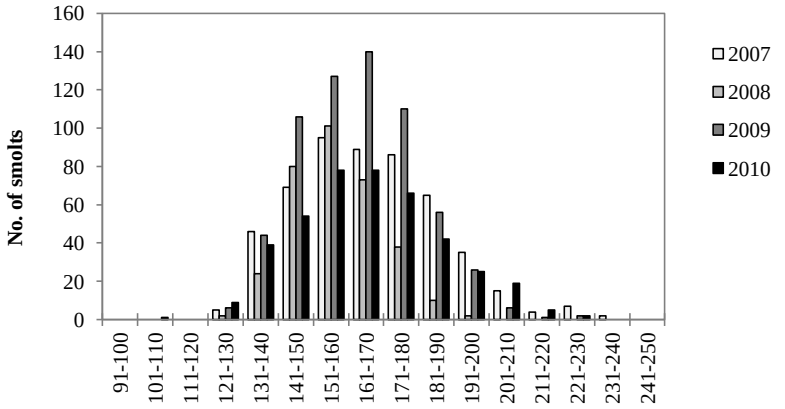
compared between the four populations. This comparison was further limited by the fact that very few S1 smolts were found in either of the Hoy populations (N=2). S3 smolts were almost absent from the BU while S4 smolts were also discounted from the analysis as they occurred so infrequently (N=9). A graphical comparison of size between different aged smolts in each burn is provided in Figure 5.3, based on pooled individual data for each age cohort across the four-year sample period. One-way ANOVA showed the S1 smolts in the Eyrland burn were significantly larger than those in the Bu burn ($F(1,199) = 54.86$, $p < 0.001$). Similarly, one-way ANOVA indicated that the size of S2 smolts was significantly different between each population ($F(3,978) = 73.18$, $p < 0.001$). Post hoc testing showed that S2 smolts were largest in the Eyrland burn, followed by those in the Bu, Ore and Whaness. Finally, one-way ANOVA also significant variation in the size of S3 smolts between each population, being largest in the Eyrland burn, followed by Ore then Whaness ($F(2,222) = 93.92$, $p < 0.001$). Therefore, in same aged smolts, growth rate in the two mainland populations was faster than in the two Hoy populations. Between the mainland populations, growth of smolts from Eyrland exceeded that from the Bu, while in Hoy populations, growth in the Ore burn exceed that in Whaness.

The oMFL (all ages) increased with stream size (measured as catchment area), as shown in Figure 5.4. Regression analysis showed that this relationship was significant ($df = 3$, $R = 0.953$, $p = 0.047$) and explained 90.9% of the variation in mean smolt size between the four burns. There was no relationship between stream size and MSA between the four populations ($df = 3$, $R = 0.370$, $p = 0.630$).

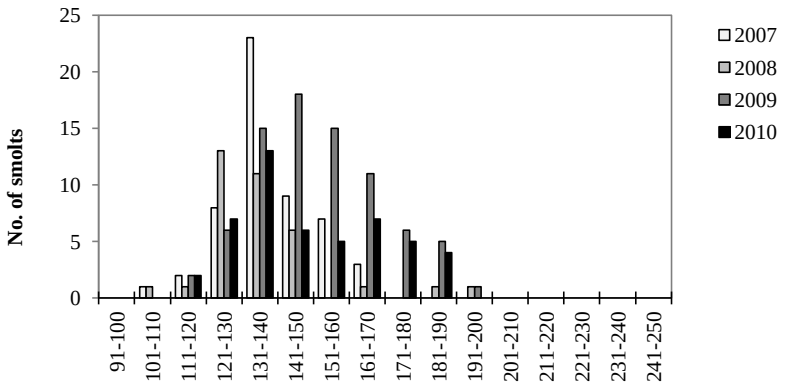
Table 5.1: Summary of smolt size and age data (±se) obtained from the burns of Eyrland, Bu, Ore and Whaness, 2007 - 2010. Eyrland data derived from downstream trap surveys, data from all other burns obtained by electrofishing. All means are for individual fish. Where no SE is shown, N = 1.

Burn	Year	N	MSA (yrs)	oMFL (mm)	Min. (mm)	Max. (mm)	S1s		S2s		S3s		S4s	
							%	oMFL	%	oMFL	%	oMFL	%	oMFL
Eyrland	2007	519	1.9 ± 0.02	166.6 ± 0.9	126	233	20.2	144.0 ± 1.0	74.1	169.3 ± 1.7	5.8	185.8 ± 2.2	-	-
	2008	333	2.0 ± 0.03	157.1 ± 0.7	125	193	4.5	151.6 ± 3.6	91.9	159.4 ± 1.4	3.6	162.3 ± 3.4	-	-
	2009	624	2.0 ± 0.02	163.0 ± 0.7	124	225	1.0	146.0 ± 12.7	92.8	164.6 ± 1.3	6.2	191.8 ± 5.1	-	-
	2010	420	2.1± 0.05	165.6 ± 1.0	101	222	17.4	138.9 ± 1.9	59.0	166.5 ± 2.1	23.6	184.0 ± 3.6	-	-
	total	1896	2.0 ± 0.02	163.1 ± 0.7	-	-	10.8	143.3 ± 0.9	79.5	166.5 ± 0.3	9.8	184.7 ± 2.7	-	-
Bu	2007	53	1.3 ± 0.05	139.0 ± 1.7	110	169	80.8	134.9 ± 1.7	19.2	154.5 ± 3.7	0	-	-	-
	2008	35	1.2 ± 0.06	135.2 ± 3.0	102	197	88.0	132.3 ± 1.7	12.0	183.3 ± 15.1	0	-	-	-
	2009	79	1.8 ± 0.06	150.9 ± 1.9	120	194	22.7	133.6 ± 1.9	74.2	158.6 ± 2.2	3.1	155.5 ± 1.9	-	-
	2010	49	1.7 ± 0.08	148.5 ± 2.8	118	190	38.9	129.4 ± 1.9	58.3	154.5 ± 3.2	2.8	181.0	-	-
	total	216	1.5 ± 0.04	144.9 ±1.2	-	-	57.6	133.3 ± 0.9	40.9	158.1 ± 1.7	1.5	161.0 ± 6.8	-	-
Ore	2007	56	2.1 ± 0.05	158.1 ± 2.2	129	207	2.1	129.0	77.1	157.2 ± 3.0	18.8	155.9 ± 3.1	2.1	157.0
	2008	44	2.1 ± 0.05	147.5 ± 1.9	122	172	0	-	88.1	146.0 ± 2.1	11.9	146.8 ± 3.4	0	-
	2009	73	2.1 ± 0.03	158.0 ± 1.8	134	201	0	-	90.0	156.2 ± 1.8	8.6	169.5 ± 4.5	0	-
	2010	66	2.4 ± 0.07	156.5 ± 1.7	121	191	0	-	37.7	151.0 ± 3.0	60.7	160.4 ± 2.2	1.6	172.0
	total	239	2.2 ± 0.03	156.4 ± 0.8	-	-	0.5	129.0	72.7	153.3 ± 0.9	25.9	159.8 ± 1.7	0.9	164.5 ± 7.5
Whaness	2007	24	2.6 ± 0.12	148.8 ± 2.7	123	173	0	-	39.1	144.1 ± 4.6	56.5	150.9 ± 2.6	4.3	173.0
	2008	47	2.7 ± 0.08	146.4 ± 1.9	119	190	0	-	29.3	137.8 ± 3.4	65.9	150.2 ± 2.5	4.9	149.0 ± 6.0
	2009	44	2.5 ± 0.10	147.3 ± 2.2	122	186	2.3	133.0 ± 1.0	43.6	136.6 ± 2.2	48.7	156.3 ± 2.9	5.1	160.0
	2010	67	2.6 ± 0.07	150.5 ± 1.9	121	190	0	-	37.7	147.0 ± 3.6	59.0	150.2 ± 2.3	3.3	160.0 ± 3.0
	total	182	2.6 ± 0.04	148.5 ± 1.1	-	-	0	133.0	37.4	141.9 ± 1.8	58.3	151.5 ± 1.3	4.3	158.7 ± 3.4

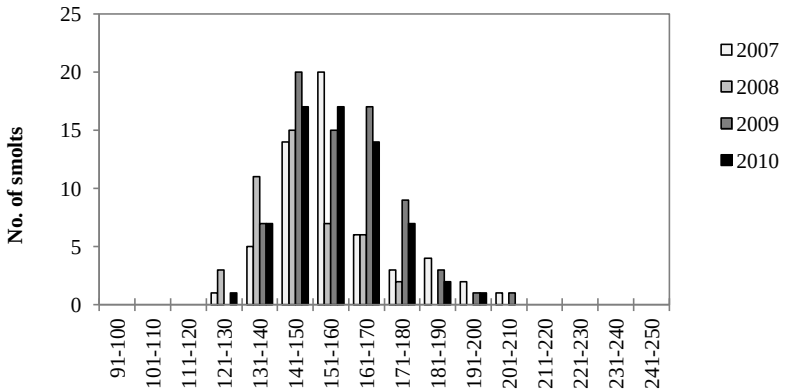
Eyrland



Bu



Ore



Whaness

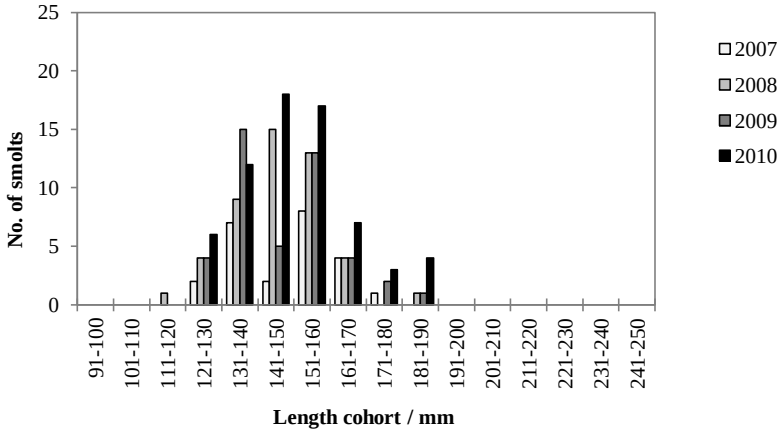


Figure 5.1: Length frequency distribution for smolts (all ages) sampled from the burns of Eyrland, Bu, Ore and Whaness in each sample year (2007 – 2010).

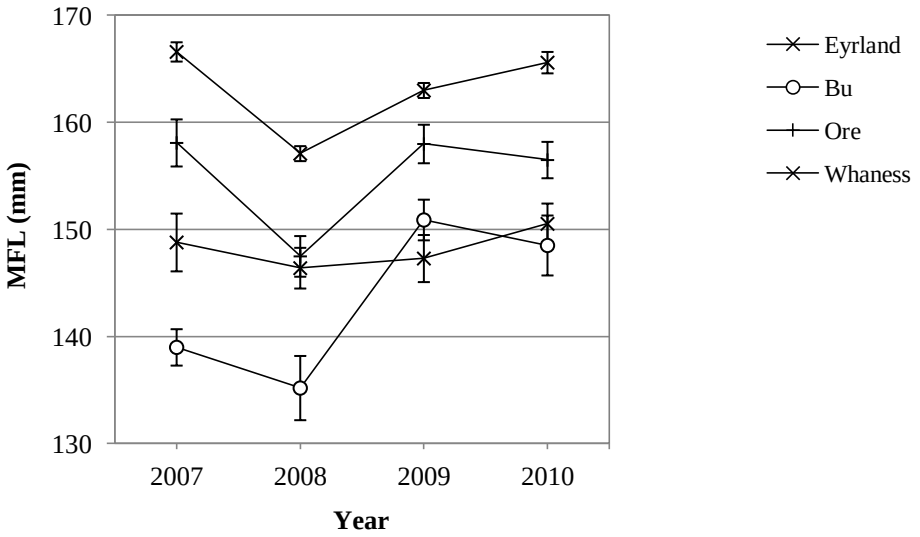


Figure 5.2: Annual oMFL (± se) of individual smolts (all ages) sampled from the burns of Eyrland, Bu, Ore and Whaness in each sample year, 2007 – 2010.

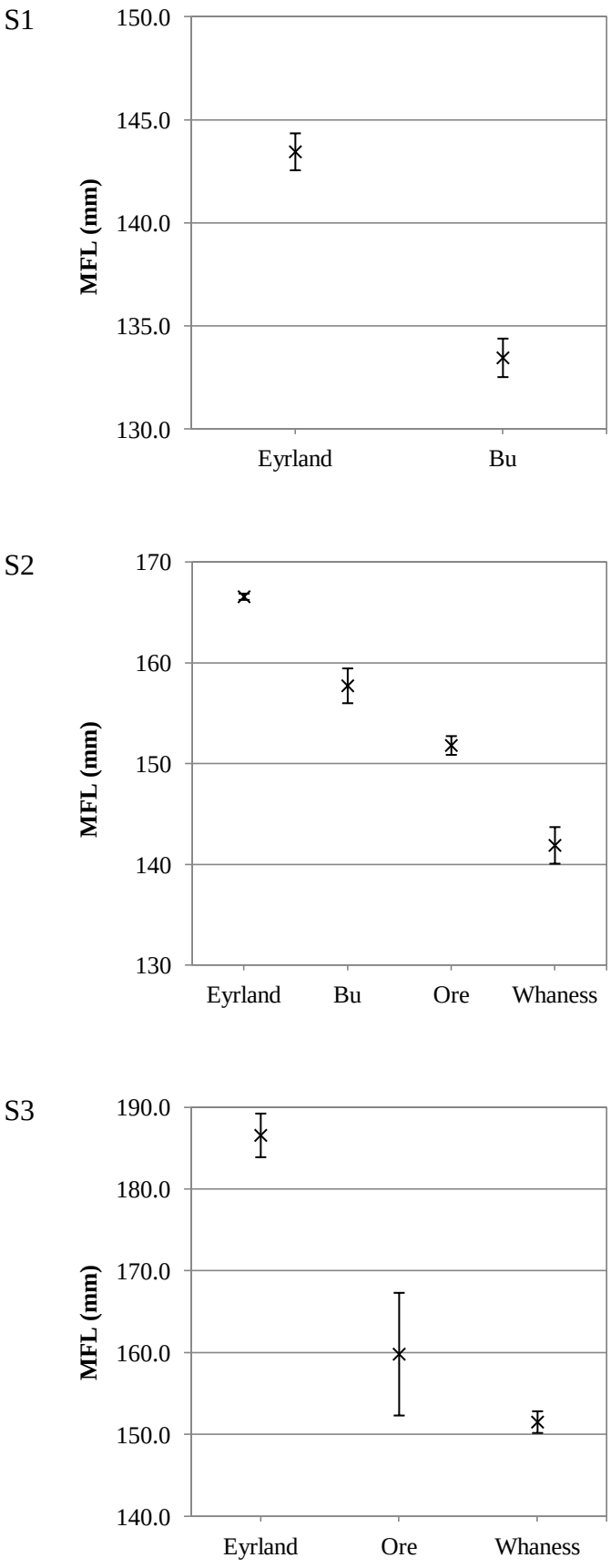


Figure 5.3: Comparison of oMFL (± se) in S1, S2 and S3 smolts sampled from the burns of Eyrland, Bu, Ore and Whaness. oMFL calculated using the pooled data from each age cohort recorded over the entire sample period, 2007 – 2010.

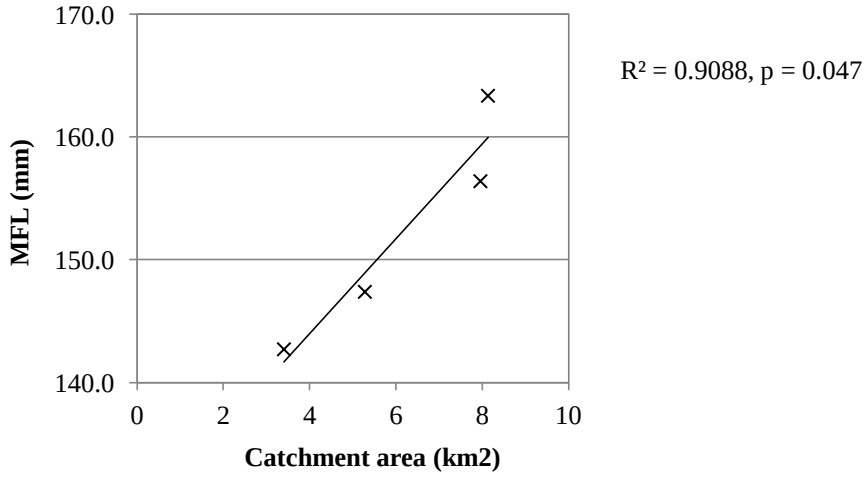


Figure 5.4: Regression analysis of the relationship between smolt size (oMFL) and catchment area in the burns of Eyrland, Bu, Ore and Whaness. MFL calaculated from pooled data for all individual smolts (all ages) sampled from each population over the sample period, 2007 – 2010.

5.3.2 Annual growth increments

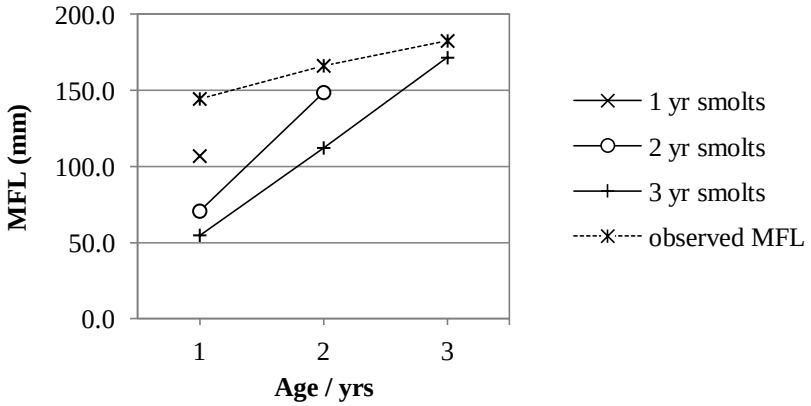
Growth curves for each smolt age cohort in each of the four populations are shown in Figure 5.5. For comparative purposes, B-growth was removed in the year of migration to obtain the size at the end of the last winter annulus, although the oMFL (size at sampling) for each age cohort is also shown. It is important to note that the oMFL line describes the mean size at time of sampling for each of the different age cohorts. It does not represent a growth curve. Figure 5.6 illustrates the annual growth increments achieved by S1, S2 and S3 smolts in each of the three populations. This clearly shows that annual growth was greatest in S1 smolts and decreased with age. Analysis using one-way ANOVA showed that the difference between annual growth increments in different aged smolts was significantly different in each population. The results of these analyses are shown in Table 5.2. This confirms that in each of the four sample populations, trout which smolted at a younger age had grown faster in freshwater.

In the mainland populations, S1 smolts were larger than S2 smolts were at age one. However, in the Eyrland population, S1 smolts were significantly smaller than S3 smolts were at age two ($F(1,196) = 33.36$, $p < 0.001$). A similar comparison was not possible in the other populations because of the rarity of S3 and S1 smolts in the Bu and Hoy populations, respectively. S2 smolts were larger at migration than S3 smolts were one year prior to migration (Ore: $F(1,215) = 185.29$, $p < 0.001$; Whaness: $F(1,154) = 218.64$, $p < 0.001$).

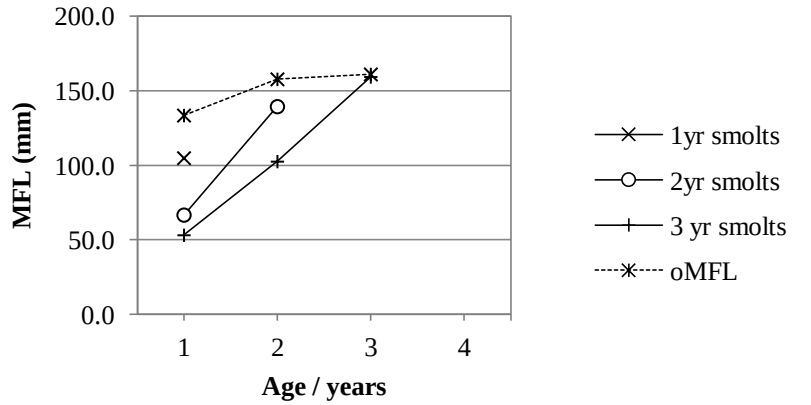
Table 5.2: Comparison (one-way ANOVA) of annual growth increments between different aged smolts in the burns of Eyrland, Bu, Ore and Whaness. Comparisons based on pooled data for each of the main smolt age cohorts over the sample period, 2007 – 2010. Post hoc testing used Fishers LSD.

Burn	**Growth increment**	**One way ANOVA result**	**Order (post hoc)**
Eyrland	1st yr	$F(2,880) = 249.10$, $p < 0.001$	S1 > S2 > S3,
	2nd yr	$F(1,759) = 58.63$, $p < 0.001$	S2 > S3
Bu	1st yr	$F(1,158) = 234.67$, $p < 0.001$	S1 > S2
Ore	1st yr	$F(1,215) = 60.63$, $p < 0.001$	S2 > S3
	2nd yr	$F(1,215) = 84.34$, $p < 0.001$	S2 > S3
Whaness	1st yr	$F(1,154) = 85.68$, $p < 0.001$	S2 > S3
	2nd yr	$F(1,154) = 72.81$, $p < 0.001$	S2 > S3

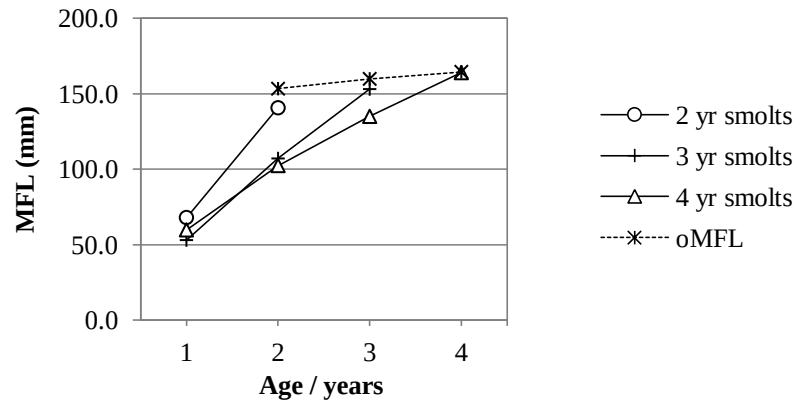
Eyrland



Bu



Ore



Whaness

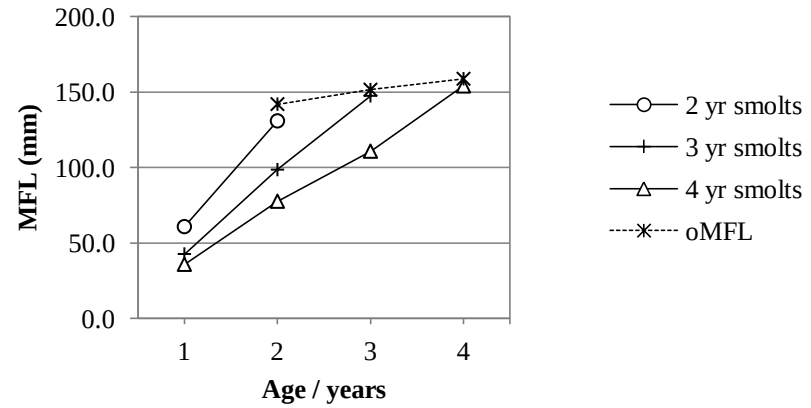
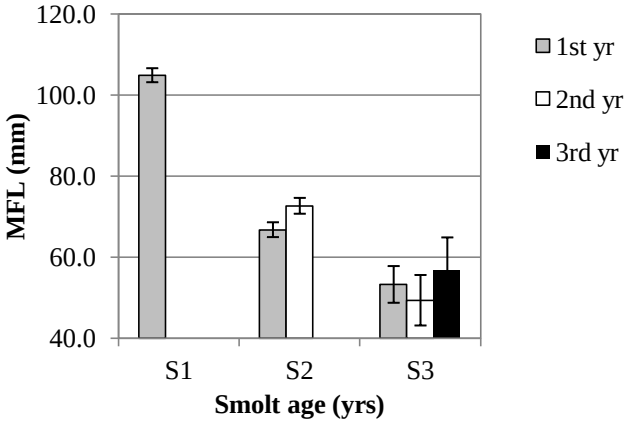


Figure 5.5: Back calculated growth curves for different aged smolts sampled from the burns of Bu, Ore and Whaness, 2007 – 2010. Size estimates based on pooled individual data for each age cohort over the entire sampling period. The dotted line indicates the oMFL of each age cohort at the time of sampling and in most cases exceeds the cMFL in the year of migration, due to B-growth.

Eyrland

Bu



Ore

Whaness

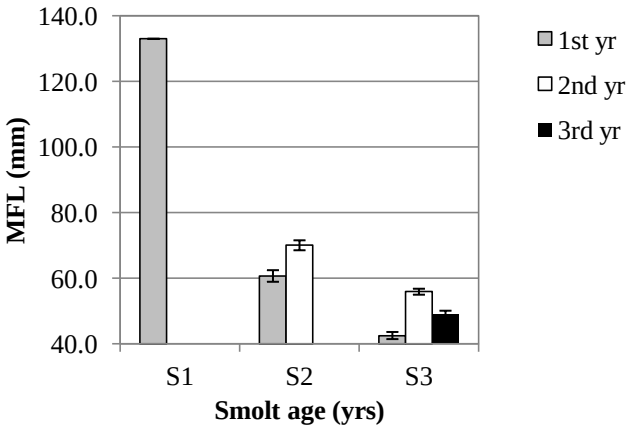


Figure 5.6: Annual growth increments (MFL±se) for S1, S2 and S3 smolts sampled from the burns of Eyrland, Bu, Ore and Whaness, based on pooled individual data, 2007 - 2010.

5.3.3 B-growth

Scale reading revealed that B-growth, defined as the difference between the cMFL and oMFL, occurred in smolts from each of the four populations (see Appendix Q for scale images). While a widening of the circuli outside the last winter check was observed as early as March in some smolts, it was generally late April when B-growth became a more frequent characteristic and greater in extent. Average B-growth (in terms of length and weight increase) exhibited by each smolt age cohort in each population is detailed in Table 5.2. Smolt length – weight relationships for each population are shown in Appendix R. GLM analysis revealed that the expression of B-growth varied between significantly between populations, age and sample year, with significant interactions between year and burn and between year and age (Table 5.4).

The extent of B-growth achieved by same aged smolts between the four populations appeared to be related to the general freshwater growth rate. In S2 smolts (well represented in all four populations) average B-growth was significantly greater in the faster growing mainland populations than in the slower growing Hoy populations (one-way ANOVA, $F(3,983) = 11.15$, $p < 0.001$). As shown above, B-growth also varied significantly between age cohorts in each population, with younger smolts exhibiting

Table 5.2: Mean B-growth exhibited in different smolt age cohorts in the burns of Eyrland, Bu, Ore and Whaness, 2007 - 2010. B-growth in weight (g) was calculated using the length-weight relationship shown for each population, where y = weight in g and x = length in mm.

Burn (length-weight relationship)	**Smolt age (yrs)**	**N**	**cMFL (mm)**	**oMFL (mm)**	**B-growth (mm)**	**B-growth (g)**
Eyrland *y = 0.0036x2 - 0.4339x + 17.825*	1	122	107.0	144.5	37.5	17.7
	2	685	148.7	166.3	17.6	12.3
	3	76	171.6	182.6	9.5	9.3
Bu *y = 0.002x2 + 0.0576x - 16.566*	1	78	104.9	133.5	28.6	15.3
	2	82	139.4	157.7	18.3	11.9
Ore *y = 0.0049x2 - 0.8167x + 47.38*	2	160	140.7	153.3	12.6	7.9
	3	57	153.0	159.7	6.7	4.8
	4	2	163.9	164.5	0.6	0.5
Whaness *y = 0.0043x2 - 0.6486x + 35.43*	2	61	130.8	141.9	11.1	5.8
	3	95	147.4	151.5	4.1	2.6
	4	7	154.0	158.8	4.8	3.3

Table 5.4: Results of GLM analysis of the role of burn, year and smolt age as fixed factors on the expression of B-growth in smolts sampled from the burns of Eyrland, Bu, Ore and Whaness, between 2007 – 2010, inclusive.

Source	DF	Adj SS	Adj MS	F-Value	P-Value
Burn	3	2882	960.6	7.29	0.000
Year	3	7579	2526.5	19.16	0.000
Age	2	26622	13311.1	100.96	0.000
Burn*Year	9	11011	1223.4	9.28	0.000
Year*Age	6	4019	669.8	5.08	0.000
Error	1392	183522	131.8		
Lack-of-Fit	12	2506	208.8	1.59	0.088
Pure Error	1380	181016	131.2		
Total	1415	319312			

greater B-growth on average than older smolts. The resulted in the younger (smaller) smolts being able to "catch up" in terms of size with older (larger) smolts. Accordingly, the difference in mean size between different smolt age cohorts was reduced in the period between the end of the last winter annulus and the point of sampling.

While the mean amount of B-growth decreased with smolt age, smolt size also played a significant role in the expression of B-growth. Among same aged smolts, a strong inverse relationship existed in some cases between size at the end of the last winter in freshwater FL at the end of winter (cFL) and the amount of B-growth expressed subsequently, in the period up to sampling. For example, this relationship is illustrated in Figure 5.7 for specific smolt age cohorts in specific years from each population. Regression analysis of this relationship for each age cohort, sample year and population is shown in Table 5.5. This trend appeared to be strongest in the two mainland populations, where significant relationships were present in 17 out of 20 comparisons, compared to only 9 out of 16 comparisons in the Hoy burns. Therefore, in the period between the end of winter and the point of sampling, fish which were initially smaller grew more than fish which were initially larger, resulting in a similar effect to that noted above, i.e. small fish were able to catch up in size with larger fish prior to migration.

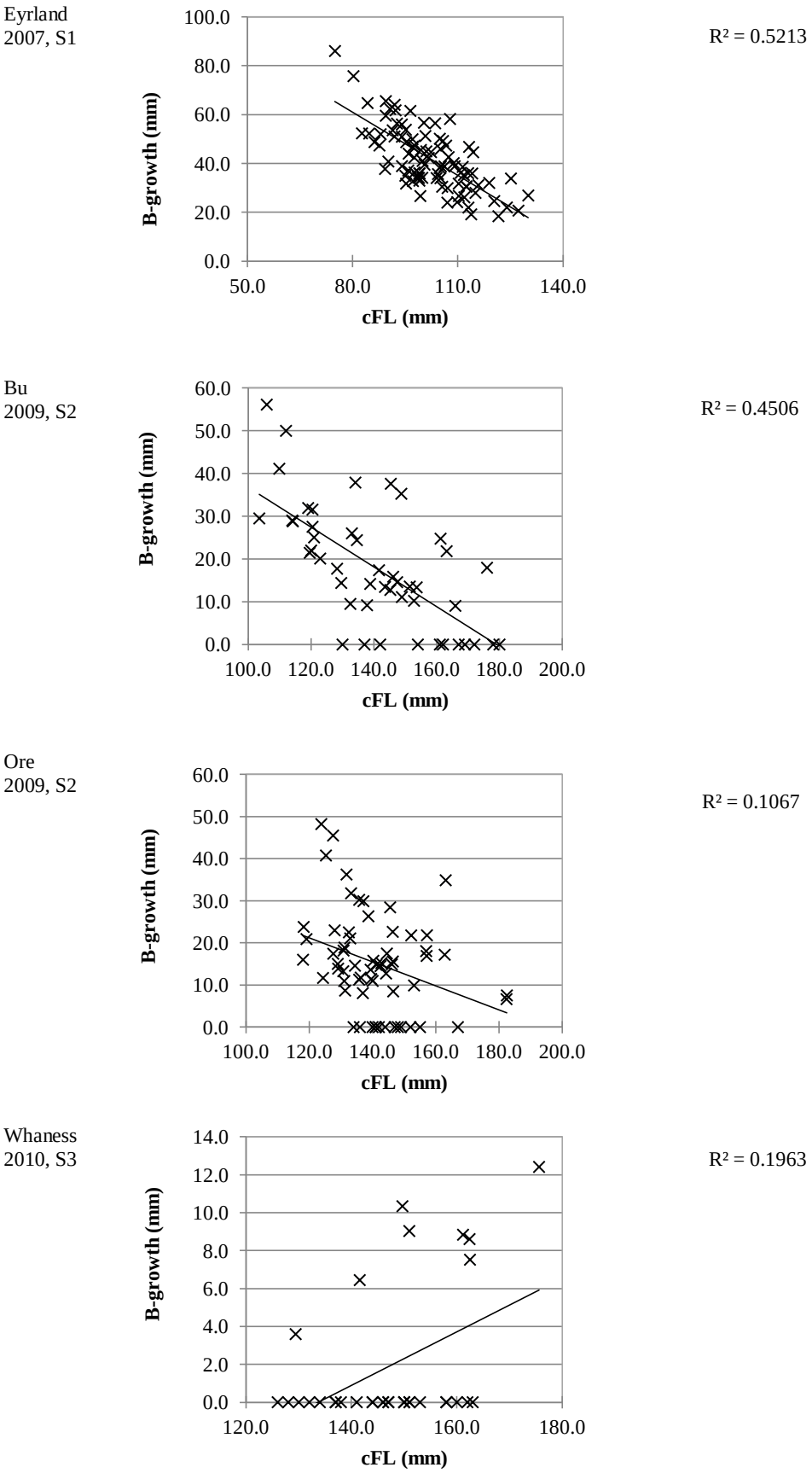


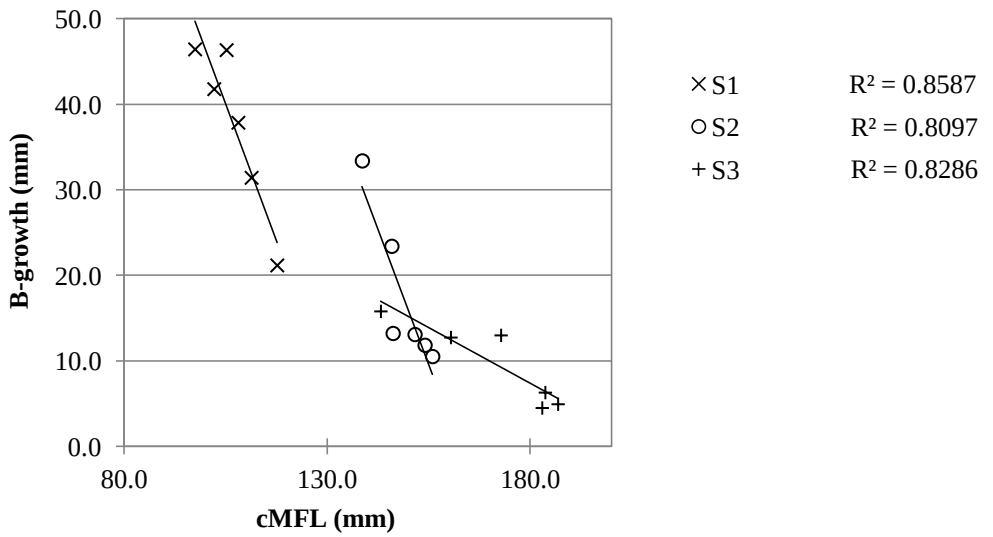
Figure 5.7: Relationship between individual cFL and B-growth in same aged smolts from selected years in the burns of Eyrland, Bu, Ore and Whaness.

Table 5.5. Results of regression analysis of the relationship between cFL and B-growth in individual smolts in each age cohort and sample year from each of the four sample populations. Significant relationships are marked with by "".*

Burn	Smolt age (yrs)	Year	Regression result
Eyrland	S1	2007	df = 90, R = 0.722, p < 0.001*
		2008	df = 4, R = 0.416, p = 0.487
		2009	No data
		2010	df = 23, R = 0.482, p = 0.017*
	S2	2007	df = 333, R = 0.615, p < 0.001*
		2008	df = 87, R = 0.698, p < 0.001*
		2009	df = 177, R = 0.652, p < 0.001*
		2010	df = 84, R = 0.540, p < 0.001*
	S3	2007	df = 25, R = 0.364, p = 0.067
		2008	df = 3, R = 0.965, p = 0.035*
		2009	df = 11, R = 0.719, p = 0.008*
		2010	df = 33, R = 0.514, p = 0.002*
Bu	S1	2007	df = 26, R = 0.643, p < 0.001*
		2008	df = 21, R = 0.880, p < 0.001*
		2009	df = 14, R = 0.847, p < 0.001*
		2010	df = 13, R = 0.909, p < 0.001*
	S2	2007	df = 9, R = 0.741, p = 0.014*
		2008	df = 3, R = 0.957, p = 0.043*
		2009	df = 46, R = 0.671, p < 0.001*
		2010	df = 20, R = 0.638, p = 0.002*
Ore	S2	2007	df = 36, R = 0.580, p < 0.001*
		2008	df = 36, R = 0.532, p < 0.001*
		2009	df = 62, R = 0.327, p = 0.009*
		2010	df = 22, R = 0.697, p = 0.002*
	S3	2007	df = 8, R = 0.541, p = 0.133
		2008	df = 4, R = 0.742, p = 0.151
		2009	df = 5, R = 0.032, p = 0.952
		2010	df = 36, R = 0.399, p = 0.015*
Whaness	S2	2007	df = 8, R = 0.351, p = 0.354
		2008	df = 11, R = 0.259, p = 0.415
		2009	df = 16, R = 0.752, p < 0.001*
		2010	df = 22, R = 0.224, p = 0.303
	S3	2007	df = 14, R = 0.597, p = 0.018*
		2008	df = 26, R = 0.285, p = 0.150
		2009	df = 18, R = 0.638, p = 0.003*
		2010	df = 33, R = 0.443, p = 0.009*

As described above, the relationship between B-growth and cFL varied between sample years. In the Eyrland and Bu populations, the comparison of cMFL in same aged smolts (S1, S2 and S3s) between sample years found an inverse relationship between the cMFL and B-growth, *i.e.* in years where MFL was less, greater B-growth occurred subsequently and vice versa (Figure 5.8). Regression analysis indicated that these relationships were significant. The same relationship was not apparent in smolts from the two Hoy populations.

Eyrland



Bu

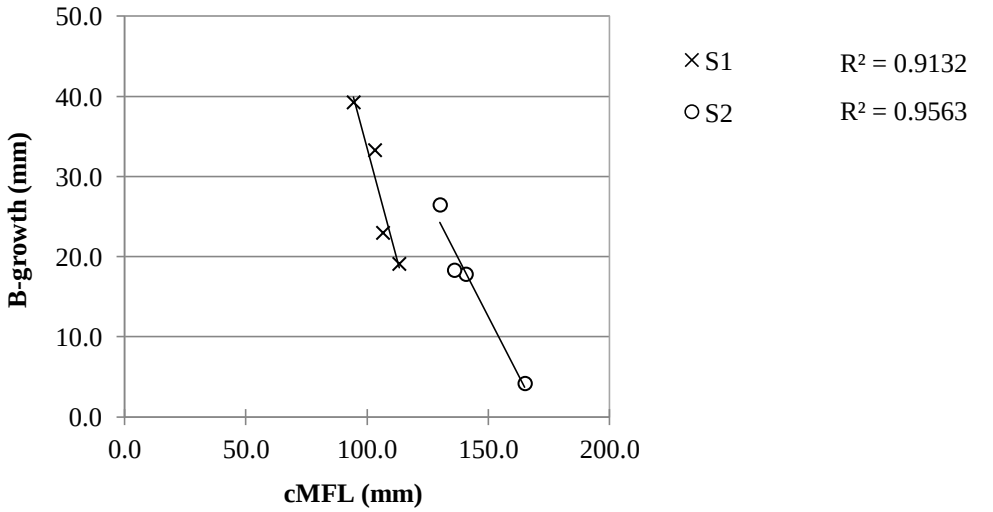


Figure 5.8: Relationship between annual cMFL and B growth in S1 and S2 smolts sampled from the burns of Eyrland and Bu, 2007 - 2010. Note that data for 2004 and 2005 are also available for the Eyrland population.

B-growth had an important effect when comparing the relative size of different aged smolts at different points in their development. It was previously stated in section 5.3.2 that in the Eyrland burn, S3 smolts were significantly larger at age two, compared to S1 smolts at the end of their first winter. However, this statement is no longer valid when B-growth is taken into account. In the Eyrland burn, the size of S1 smolts after B-growth (oMFL) was significantly larger than the MFL of S3 smolts at age two ($F(1, 196) = 85.55$, $p < 0.001$). The oMFL attained by S1 smolts ranged from 129.0mm to 143.3mm between the four populations studied here.

5.4 Discussion

This phase of fieldwork collected a large volume of data which was sufficient to characterise smolting trout from each population. Smolts from the burns of Eyrland and Bu on the Orkney mainland grew faster in freshwater relative to their counterparts in the Ore and Whaness burns on Hoy. This resulted in a lower average age at smolting in the mainland populations, which were dominated by S1 and S2 smolts, while S2 and S3 smolts were prevalent in the Hoy burns. While same aged smolts were larger in populations with a higher freshwater growth rate, overall mean smolt size (all ages) varied directly with stream size. The expression of B-growth was greatest in the youngest and smallest smolts. Initial size (at the end of winter before migration) appeared to have a strong indirect on the amount of B-growth achieved before migration. In same aged smolts, a significant year effect was observed where more B-growth occurred in years where the mean size at the end of the winter was smaller, and *vice versa*.

Smolt age and size

The mean smolt age and size for each of the four populations fitted well within the range exhibited across European populations (Jonsson & L'Abée-Lund, 1993). Smolt age ranged from one to four years (representing all smolt ages previously reported in the UK) although MSA between the four populations differed significantly. Therefore, in addition to the broad geographic trend of increasing smolt age with increasing latitude, these results showed that age may also vary significantly between populations separated only by a few miles. Mean size varied from 142.7mm (Bu) to 163.1mm (Eyrland), further demonstrating the potential for differences between closely neighbouring populations. Regional differences in smolt size have been reported in Norway (L'Abée-Lund *et al*., 1989) and Scotland (Nall, 1933). In the latter case, it was observed that on average, smolts in Orkney were smaller (and younger) relative to those in Scottish mainland populations. The same trend was seen here in a comparison of Orkney smolts to recent smolt data from the Tournaig & North Esk (Pratten & Shearer, 1983a; Wester Ross Fisheries Trust, Tournaig trap surveys, unpublished data).

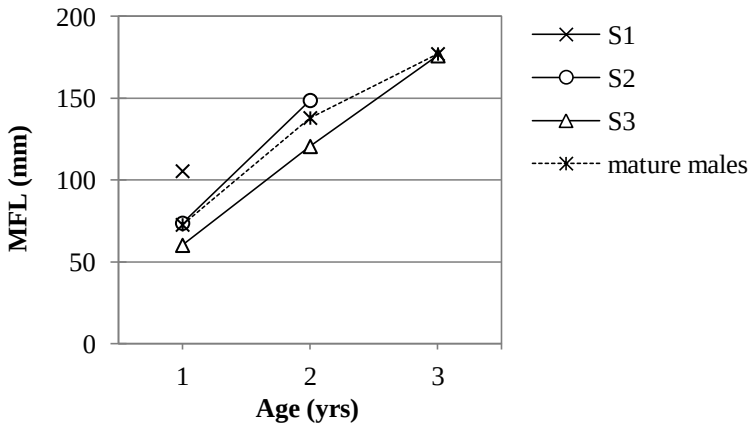
The smolt growth data collected here allow a comparison with the growth of mature resident trout detailed in Chapter 4. Growth curves for different aged smolt and mature

trout in each of the four populations are shown in Figure 5.9. In each population, the growth rate for resident mature males was within the range exhibited by different aged smolts on average. Mature males were slower growing than young smolts and faster growing than older smolts in each population. This reflects research carried out elsewhere Forseth *et al*., 1999) and clearly shows that growth rate *per se* does not determine the choice between a resident or anadromous life history, as both slow growing and fast growing individuals can migrate from a single population. As smolts from the two mainland burns were faster growing on average, they migrated at a younger age on average, relative to smolts from the two Hoy burns. As well as supporting the view that faster growing individuals migrate at a younger age and *vice versa* (Alm, 1950; Went, 1962; Pratten & Shearer, 1983a), this also highlights the role of local factors in determining growth rate and therefore smolting characteristics between closely neighbouring populations.

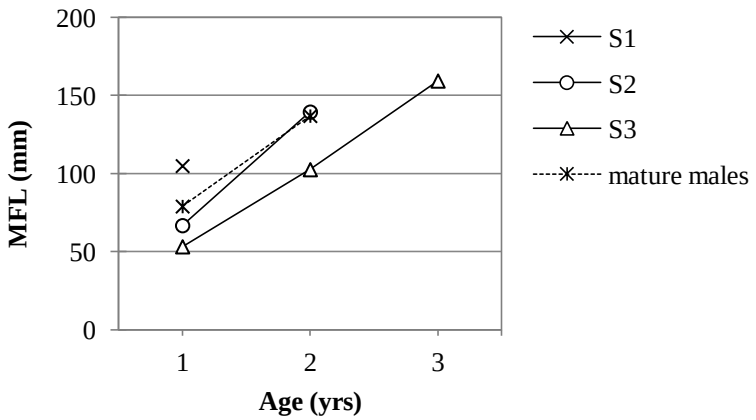
The effect of stream size

Stream size had a direct effect on the mean size of smolts (all ages) in each population. This agreed with the findings of Jonsson *et al*. (2001) who found such a relationship in streams with an annual mean discharge of less the 0.2 cumecs. All four burns studied here had an estimated annual mean discharge similar or less than 0.2 cumecs. Interestingly, the smallest smolt found over the sample period (101mm) came from the Eyrland burn, the largest of the four studied. However, the relationship between discharge and smolt size did not appear to hold for individual age cohorts. The average size of S2 smolts in the Bu, the smallest burn, was the second highest of the four populations. It was the dominance of smaller S1 smolts that caused the overall smolt size (all ages) to be least of the four populations. Therefore, the tendency for the Bu to produce younger smolts had a strong bearing on overall smolt size in that population. But why were S1 smolts most common in the Bu? It has been noted that fast growth leads to early migration and this might result in a high proportion of S1 smolts. However, S1 smolts in the Eyrland population were faster growing on average yet made up a smaller proportion of the overall smolt sample, relative to the Bu. Titus & Mosegaard (1989) found that emigration of one year old trout was common in a small, drought affected stream in the Swedish Baltic and suggested that this could be adaptive

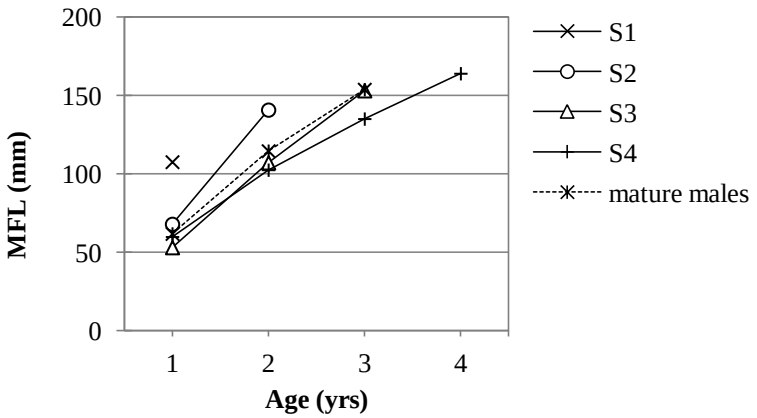
Eyrland



Bu



Ore



Whaness

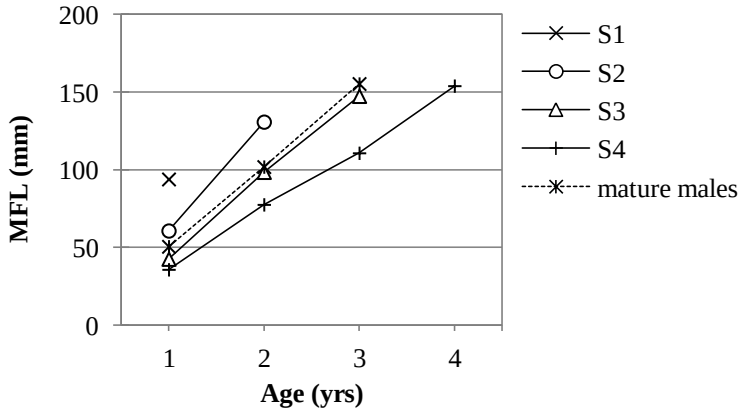


Figure 5.9: Comparison of growth curves between different aged smolts and resident mature male trout in the burns of Eyrland, Bu, Ore and Whaness. Male data collected between 2007 – 2009.

response to unstable conditions in the natal stream. However in that study it was not clear if the emigration involved true smoltification, as the salinity of the receiving "marine" environment was only 6-7ppt. Jonsson *et al*. (2001) sampled returning anadromous trout in 17 small streams in Norway which discharged into full strength seawater (~35ppt). Surviving fish which had an MSA of less than 2 years (1.2 & 1.6yrs) were found in two streams with an annual mean discharge of approximately 0.05 cumecs, which is comparable to the estimated discharge of 0.068 cumecs in the Bu. These studies along with the results obtained here, support the concept that small streams such as the Bu tend to produce younger smolts than larger streams. However if this is an adaptive response then it might be expected that each year's smolt output would be dominated by the youngest age cohorts. This was not the case in the Bu, when S2 smolts were more abundant than S1 smolts in 2009 and 2010. Jonsson *et al*. (2001) suggested that emigration at a young age might alternatively be a plastic response to adversity. The results from the Bu suggest a slightly different scenario where the dominant smolt age might simply be determined by mortality rates in fish which stay in the burn after the age of one. When survival among these older fish is good then a larger number of older smolts may appear in subsequent years. When survival is poor, *e.g.* due to drought, then smolt production in subsequent years may be dominated by younger smolts.

Between populations, mean smolt size was not related to mean smolt age. While the Eyrland burn produced the largest smolts, the Whaness burn produced the oldest smolts, on average. It might generally be expected that older smolts would be larger but in this case, the much faster growth in the mainland burns was sufficient to compensate for the lack of older smolts. In fact, S2 smolts from the Eyrland burn were significantly larger than S3 smolts from both the Ore and Whaness burns. It was also apparent that in each population, annual growth increments were largest in the youngest age cohorts and declined with age. This supports the general view that slower growth results in a higher age of migration (Jonsson & L'Abée-Lund, 1993). The difference in smolt growth rates agreed with observations made in Chapter 4 on juvenile (pre-smolting) growth in each population, where juvenile trout in the Hoy burns were slower growing than those in the mainland burns. The reasons suggested for these contrasting growth rates were differences in water temperature and quality in each burn, which in turn, affect trout growth rates and the availability of food for juvenile trout (Elliott, 1994; Kirby, 2011).

Freshwater growth

As noted earlier, faster growth in freshwater resulted in a younger smolt age, on average. In S2 smolts from each population, the size of parr at the end of the winter before migration (cFL) was directly related to both the first and second annual growth increments, *i.e.* faster growth results in larger smolts, which is perhaps not surprising. Quantifying this relationship between different populations is perhaps more interesting however. Jonsson & L'Abée-Lund (1993) found a direct relationship between the second year growth increment and size at smolting. However, whereas those authors found that second year increments of 40 – 100mm corresponded to smolt lengths of 160mm – 200mm, the present study found second year increments of between 70.1mm – 75.0mm corresponded to an oMFL of 141.9mm – 166.5mm, respectively. More data from other populations would help to further examine this relationship. The link between the first year growth increment and smolt size seen here has not been previously observed, although it has been noted elsewhere that this is a problematic comparison as the timing of first growth may vary between populations (L'Abée-Lund *et al*., 1989).

In each population, mean annual growth increments varied significantly between different aged smolts. S1 smolts attained a mean size of approximately 100mm by the end of their first winter, while S2 smolts achieved much less growth in their first year and therefore required an additional year to smolt. S3 smolts exhibited less growth again in their first year and subsequent years. An average length of approximately 100mm in the first year therefore appeared to represent a threshold past which smoltification could result. In brown trout, Økland *et al.* (1993) found that in the youngest smolt cohorts, a large proportion (>80%) migrated to sea the first spring after attaining a length of 10cm in autumn. In Atlantic salmon, Nicieza *et al*. (1991) reported a similar first year threshold of approximately 100mm for smolting at age 1, as well as a critical (*i.e.* minimum) length at smolting of approximately 130mm. That study also made the distinction that size at the end of winter and size on entering seawater are different, an important concept which is also embraced here. However, in this case it was also apparent that S3 smolts were on average larger than 100mm at age two, but did migrate. Therefore, attaining a size of 100mm did not on its own result in smoltification. The same observation was made by Økland *et al.* (1993) and was used as evidence to reject the hypothesis that smoltification accords to a universal threshold size in anadromous brown trout. However, it was also apparent here that S1 smolts had

a mean size at sampling (just prior to seawater entry) which was significantly larger than 100mm. This was a result of B-growth which had occurred in freshwater in the period leading up to sampling and was not accounted for by Økland *et al.* (1993) who used the moment at the end of the last winter annulus in freshwater as being representative of smolt size. The data presented here clearly demonstrate that B-growth had a significant role in determining smolt size in the period leading up to seawater entry, which should be considered in any debate about smolt size at seawater entry.

B-growth

B-growth in smolts was successfully quantified in each population by ensuring that smolts were sampled close to the point of seawater entry. In each population, B-growth was greatest in the youngest (and smallest) age cohorts and decreased with age. Greater B-growth in younger smolt cohorts has been reported previously (Went, 1949). However this study provided strong evidence that among same aged smolts, an inverse relationship occurred between size at the end of winter and the amount of B-growth achieved subsequently, in the period leading up to seawater entry. In this case, size and not age was the determinant of B-growth expression. The result of this process was that smaller trout were able to "catch up" in size terms with same aged trout which had initially been larger at the end of winter. Additional B-growth was at facilitated in part by the tendency for younger (smaller) smolts to migrate to sea later in the spring, so extending the B-growth period. Overall, it was apparent in this study that B-growth allowed individual fish to compensate for poor growth performance in freshwater in a last minute growth surge, proportional to the amount of growth restriction, to maximise size prior to seawater entry and hence maximise chances of marine survival. Additional evidence that size was implicated in B-growth came from the Eyrland and Bu populations. Between sample years, same aged smolts exhibited B-growth which was negatively related to their mean size at the end of winter. In other words, for a given age cohort, greater B-growth was achieved before seawater entry in years when their mean size at end winter was smaller and *vice versa.* Such an effect has not previously been reported in the literature, although Fahy (1990) argued that annual levels of B-growth varied with spring growing conditions. Variation in the annual expression of B-growth will be examined further in Chapter 6.

The inverse relationship between size and B-growth was seen in each of the four study populations, although in to differing degrees. In the same age cohort, smolts from populations where freshwater growth was faster, *e.g.* Eyrland, exhibited greater B-growth relative to those from slower growing populations, *e.g.* Whaness. In addition, the trend was not as consistent between years and age cohorts in the Hoy burns relative to the mainland burns. This could have been because B-growth in those populations was less, particularly because smolts here were older and slower growing. Statistical analyses would also have been improved by greater sample sizes in some cases (*e.g.* 2007, Whaness, S2 smolts, N = 9).

The rarity with which B-growth occurs in the literature on sea trout ecology is striking. The only author to routinely report and quantify B-growth was Edward Fahy, the author of various reports on Irish sea trout populations on behalf of the Department of Fisheries and Forestry (Fahy 1979; 1980; 1981). B-growth increments of between 2.0 and 3.6cm in S2 smolts from the Cummeragh system were reported (Fahy, 1990). Standard scale reading texts, *e.g.* Elliott & Chambers (1996), note the presence of a "run-out" phase, defined as the region between the last winter annulus and the start of the period at sea. However, it is also noted that discerning the run-out phase in scales from adult sea trout is "usually too difficult". No mention of run-out is made in the section on reading and interpretation and it is the author's opinion that in general, this phase is lumped together with the marine growth phase. The implication of ignoring B-growth (or run out) in back calculation methodologies is that smolt size is underestimated if the point of seawater entry is taken to be the end of the last winter annulus. This study has shown that B-growth can cause a significant increase in size prior to seawater entry, particularly in the youngest (& smallest) smolts. Here, S1 smolts (N = 122) sampled in the Eyrland burn increased their size (FL) by an average of 35% between the end of the last winter and the point of sampling, just prior to seawater entry. A few individuals increased in length by almost 100% during the B-growth phase.

Therefore, if commonly used scale reading methodologies such as Lea (1910), Jonsson & Stenseth (1976) and Elliott & Chambers (1996) take no account of B-growth, then studies employing these methodologies may be flawed, as described above. Such studies include some of the widely cited examples already mentioned, *e.g.* Økland *et al*. (1993), L'Abée-Lund *et al*. (1989), Jonsson & L'Abée-Lund (1993) and Jonsson *et al*.

(2001). Indeed the same risk in Atlantic salmon has been noted by Heidarsson *et al*., (2006). In this study, B-growth was greater in younger smolts. Across the European range of *Salmo trutta*, MSA increases with latitude (Jonsson & L'Abée-Lund, 1993). It follows therefore that B-growth will be a more significant feature of growth in southern (younger) populations relative to northern (older) populations. Associated with this however is a greater potential for error in the estimation of smolt size by back-calculation. Clearly this possibility has to be tested in other regions to ascertain its significance but if it proves to be the case that B-growth is common and that it has not been properly accounted for, then our present understanding of anadromous trout ecology is eroded somewhat. It would certainly suggest a fresh examination of the relationship between size and migration in anadromous trout across its range. Studies which focus on marine growth rates might also consider the implications of B-growth, considering that the marine growth phase is generally assumed to begin following the last winter annulus in freshwater. Proper accounting for B-growth is clearly a problematic goal when dealing with scales from mature sea trout. This study generated excellent B-growth data by sampling smolts at the moment of seawater entry, which is not always possible, particularly in larger river systems. Modern biochemical methods involving the chemical analysis (Sr:Ca ratios) of scale composition, *e.g.* Limburg *et al*. (2001), provide an alternative to pinpoint the time of sea entry and may therefore allow the more accurate estimation of size, but are time consuming and costly.

B-growth & size at smolting

This study found that on average, S3 smolts were significantly larger at age two than S1 smolts were at the end of their first winter. The same observation was made in a Norwegian study by Økland *et al.* (1993) and was used as evidence to reject the theory of a threshold size for smolting in *Salmo trutta*. However, if the contribution of B-growth is considered the same comparison finds that S1 smolts were in fact significantly larger on average than S3 smolts were at age two. This in contrast tends to support the notion of a threshold size theory. In this study, the mean size (including B-growth) of all smolt age cohorts did not exceed 130mm in any year apart from the year in which migration to sea occurred. If size is a significant determinant of whether or not migration occurs, then further analysis of *individual* size is required, as the mean size of different age cohorts or populations does not account for the behaviour of all individuals. The Eyrland population lends itself to further study as it was the populations for which the greatest amount of data was collected and perhaps more

importantly, three age cohorts of smolts (S1, S2 and S3) were well represented, allowing a more valid comparison of size and migratory behaviour between cohorts (only two age cohorts were well represented in each of the other three populations).

In summary, in this chapter it has been demonstrated that smolts from the burns of Eyrland and Bu on the Orkney mainland grew faster in freshwater relative to their counterparts in the Ore and Whaness burns on Hoy. This resulted in a lower average age at smolting in the mainland populations, which were dominated by S1 and S2 smolts, while S2 and S3 smolts were prevalent in the Hoy burns. While same aged smolts were larger in populations with a higher freshwater growth rate, overall mean smolt size (all ages) varied directly with stream size. B-growth, rarely considered in the literature on salmonid species, was successfully quantified in smolts from each population. The expression of B-growth was greatest in the youngest and smallest smolts. Initial size (at the end of winter before migration) appeared to have a strong indirect on the amount of B-growth achieved before seawater entry. A significant year effect was observed in smolts from the Eyrland and Bu populations where in years where mean size was smaller at the end of winter, greater mean B-growth occurred subsequently, and *vice versa*. Although rarely studied, it was argued here that the significant effect of B-growth on smolt size should be considered in the examination of smolt size and marine growth rates in anadromous trout populations. In the following chapter, data from the Eyrland burn is studied in more detail. This will focus on migratory behaviour in smolts and the environmental stimuli that influence their downstream migration. A further examination of B-growth will also take place to better understand its significance within the freshwater growth phase and its impact on size at smolting.

CHAPTER 6. SMOLTS FROM AN ANADROMOUS BROWN TROUT POPULATION: TRENDS IN FRESHWATER GROWTH AND MIGRATION

6.1 Introduction

Smolts of both salmon and trout lend themselves to population studies, as their seaward movement occurs over a discrete time period each spring and a well placed (and designed) fish trap can effectively sample the fish passing downstream from all areas of the catchment above. In large rivers only a small sample of the smolts might be caught, owing to difficulties in entraining fish from the whole width of the river-course, but in smaller rivers and burns it is, at least in theory, possible to catch almost the entire run. Among anadromous trout populations, trap-derived data is used to examine a range of characteristics. Catch data, used in combination with measures of trap efficiency, are commonly used to estimate smolt productivity for areas upstream of the trap (Laughton *et al.*, 2008). Estimates of smolt production in anadromous brown trout populations vary from 1.2 smolts per $100m^2$ in a Norwegian river with a sympatric population of Atlantic salmon to 19.8 smolts per $100m^2$, in a small Danish stream with no salmon present (Hesthagen *et al*., 1986; Rasmussen, 1986). Smolt size and age data provide an indication of growth conditions in freshwater and may also be used to predict future trends in marine growth rate, age at maturity and longevity (Jonsson & L'Abée-Lund, 1993). Trap data also provide insight into how the environment influences their downstream migration to sea (Byrne *et al*., 2004). Estimation of the outgoing smolt population also represents the starting point for the measuring marine survival in anadromous salmonids (Euzenat *et al*., 2006; Gargan *et al*., 2006). The aquaculture industry in particular has driven research into the physiological aspects of smoltification, a key stage in the culture of salmonids (Boeuf, 1993). While in general the smolting process is well understood, there is still scientific interest in the migratory behaviour of brown trout, which as described in Chapter 1, exhibits great flexibility. In their summation of the Cardiff Sea Trout Conference held in 2004, Milner *et al*. (2006) highlighted the need to *inter alia* better understand the role of the environment and genetics in determining the sea-going habit of sea trout and also highlighted the need to investigate life history strategies in different stream types and in different geographic areas.

Byrne *et al*. (2004) noted the presence of pre-migration regulating factors, such as photoperiod and water temperature, and within migration controlling factors, such as water level, which might influence day to day movements of smolts. Regulating factors influence the development of smolts and the start of their downstream movement. The hypothesis that water temperature plays a significant role in initiating the downstream movement of smolts is underpinned by observations that with increasing latitude, smolt migrations occur later in the year. In southern Europe, *e.g.* France and Spain, peak migration generally occurs in April, while in northern Norway it may not occur until June or July (Caballero *et al*., 2006; Euzenat *et al*., 2006; Jensen *et al*., 2012). While attempts have been made to model the optimal timing of smolt migration (Bohlin *et al*., 1993) it is recognised that this will vary between populations and is also subject to certain local factors, *e.g.* the presence of obstacles to migration (Bohlin *et al*., 1993; Jensen *et al*., 2012).

Smolt size and age characteristics have been reported in many populations across Europe (Fahy, 1981; L'Abée-Lund *et al*., 1989; Euzenat *et al*., 1999; Jonsson *et al*., 2001) and the results of smolt sampling in four Orkney populations were discussed in Chapter 5. It is also widely reported that in individual populations, smolt size and age characteristics vary as the smolt migration progresses through the spring period. Generally, larger, older smolts move downstream earlier in the smolting period than smaller, younger smolts (Euzenat *et al*., 1999; Bohlin *et al*., 1993). It is suggested that this occurs because osmoregulatory ability in smolts improves with size (Hoar, 1988) and smaller smolts delay their passage into salt water in order to achieve additional size to better cope with the transition to sea. However it has recently been reported that in a Norwegian population of brown trout, which is incidentally sympatric with anadromous Atlantic salmon and Arctic char, an early run of small smolts also occurs (Jensen *et al*., 2012). It is speculated that these smolts may comprise fish with the highest metabolic rate which drives them to seek a more productive environment (the sea) as soon as possible in the smolt window. The possible effect of the sympatric salmon and char populations on the downstream migration of trout was unknown.

Despite this, it is clear that some, if not the majority of smolts which are smaller at the start of the migration period, delay their departure, during which time they achieve additional growth. Smolts which achieve this additional growth were first recognised by Went (1938) in a study of Atlantic salmon in Ireland and were termed B-type smolts,

as opposed to A-type smolts, which exhibited little or no such growth and migrated to sea very shortly after the last winter annulus. The same pattern was observed in sea trout smolts Went (1949) and this type of growth has also been referred to as B-growth by some (Fahy, 1990) and "plus" growth by others (Pratten & Shearer, 1983a). The terms B-type smolt and B-growth are preferred here. In a study of sea trout smolts from the Owengowla River, Went (1949) estimated that the amount of B-growth decreased with increasing age. Only one S1 smolt was sampled which achieved 48.3mm of B-growth. S2 smolts (N = 282) averaged 27.9mm, S3 smolts (N = 67) 17.8mm and S4 smolts (N = 1) 30.5mm. Fahy (1990) found that S2 smolts from the Cummeragh system in Ireland attained between 20mm and 36mm in B-growth immediately prior to migration. In this study, B-type smolts were detected in a number of Orkney populations (Chapter 3) and this aspect of freshwater growth was studied in detail in four populations (Chapter 5). In common with the findings of Went (1949), average B-growth decreased with smolt age in each of the four populations. Despite the relatively detailed work done in Ireland, particularly by A. E. J. Went, the subject of B-growth rarely appears in the literature on *Salmo trutta*. This study therefore represents a contemporary examination of the issue and potentially refreshes the debate regarding a threshold size for smolting in brown trout populations, supported by some (Fahy, 1985) and rejected by others (Økland *et al*., 1993). Further examination is required however to expand on the work by Fahy (1990), which also described the impact of water temperature on mean B-type growth increments in trout smolts. Other aspects of freshwater growth, *e.g.* annual growth increments, are relevant in the study of smolt size and age characteristics. In a review of European data, Jonsson & L'Abée'Lund (1993) found that second year growth in freshwater was negatively associated with latitude and positively associated with mean size of S2 smolts. These trends and features were considered in Chapter 5 but further analysis might feed usefully into the examination of freshwater growth and its relationship to smolt production.

This chapter considers these aspects of anadromous trout populations using smolt data collected from the Burn of Eyrland between 2004 and 2010. The main research aims were:

- To estimate the number of smolts emigrating from the Eyrland system each year;
- To estimate smolt production in terms of smolts per unit area of wet habitat;

- To determine which environmental factors had a significant effect on the downstream migration of smolts;
- To characterise the size and age of smolts from the Eyrland system;
- To quantify the expression of B-growth in different aged smolts and determine the relationship between B-growth and the size of parr at the end of the winter prior to migration; and
- To determine if a target smolt size exists in this population which influences the age at which individuals migrate to sea

The methods and results are detailed in the following sections.

6.2 Methods

The reader is referred to Chapter 2 for a detailed description of methods used in this phase of work. Summaries are provided below. The Eyrland burn has been described previously in Chapter 4.

6.2.1 Smolt sampling

Smolt sampling in the Eyrland burn was carried out between 2004 and 2010, inclusive. Descriptions of the traps used over this period were provided in Chapter 2. Trap data collected prior to 2007 were used for information on run-timing, but abundance figures from those years were treated with caution, as the trap efficiency was almost certainly lower than that of the Wolf type trap operated between 2007 and 2010. This was borne out by the consistently higher catches made from 2007. Trout were classified according to the scheme described in Chapter 2, *i.e.* "B", "1S", "2S" or "3S". Fish in the 2S and 3S category were classified as smolts for the purposes of subsequent data analysis. Fish in the B and 1S category were not categorised as smolts and therefore were not included in the analysis of smolt data.

Smolt productivity was estimated as number of smolts produced per $100m^2$ of wet area of burn. Wet area of the burn was judged to include the main branch of the burn and a further 500m up each of the three main tributaries, which comprised a total burn length of 4.96km. The average wet width of the burn was 2.05m ± 0.07m (se), which was the average width of all timed electrofishing survey sites, described in Chapter 4. The overall wet area of burn was therefore $12400m^2$.

6.2.2 Fish processing

All smolts were processed according to the methods for fish processing found in Chapter 2. Tagging, the procedure for which was described in Chapter 2, was carried out in years 2004 – 2007, inclusive.

6.2.3 Temperature data

Air temperature data for Orkney were kindly provided by the Marine Services Department, Orkney Islands Council. Following the method of Fahy (1990), the spring growing period in each year was defined as the number of days when air temperature was 5.6°C or greater in the period from February to May, inclusive.

Water temperature was recorded using Gemini Data Loggers (TinyTag Plus), installed adjacent to the fish trap and anchored to the stream bed. Initially, temperature was recorded at 6 hour intervals but this was subsequently changed to one hour intervals. Data were downloaded using a direct serial cable connection to laptop using Gemini Logger Manager (V2.2).

6.2.4 Scale reading

Scale reading was carried out according to the method described in Chapter 2.

6.2.5 Data analysis

Data analysis was carried out using SPSS, versions 14 and 16. Comparison of fork length data was carried out using ANOVA. A p-value of 0.05 was used unless stated otherwise. Where more than two groups were being compared a post-hoc test (Fisher's LSD) was used to identify significant differences between the mean values of individual groups. Regression analysis was carried out using Microsoft Excel.

6.3 RESULTS

6.3.1 Annual smolt trap catches

A summary of each year's catch in the Eyrland smolt trap is provided in Table 6.1. Daily smolt catch, water level and water temperature in each year's survey are illustrated in Figure 6.1. The smolt catch between 2004 and 2006 varied between 92 and 155. The catch of 92 smolts in 2005 comprised additional samples obtained by electrofishing samples, as only 28 smolts were caught in the trap. Annual catches increased following the installation of the Wolf trap in 2007 and over the four year period to 2010 varied from 333 to 624, with an average annual catch of 474 smolts. The smolt catches from 2007 to 2010 equated to a productivity of 2.7 – 5.0 smolts per $100m^2$ of wet area in the Eyrland burn. Detailed results from each year of trapping are contained in Appendix N.

Table 6.1: Annual catch of brown trout smolts in the Burn of Eyrland trap, 2004 – 2010. Smolts included those fish classified as 2S or 3S in the classification scheme described in the methods section. "nd" = no data. Productivity based on a wet area of habitat in the Eyrland burn of 12400m^2.

Year	Total Catch	Total Smolts	Date (5% run)	Date (95% run)	Productivity (smolts 100m^{-2})
2004	187	148	10/4	17/5	1.2
2005*	114	92	nd	nd	0.7
2006	257	155	30/3	3/6	1.3
2007	644	519	7/4	14/5	4.2
2008	467	333	25/4	20/6	2.7
2009	673	624	8/4	9/5	5.0
2010	530	420	18/4	28/5	3.4

* trap catch of 28 was augmented by electrofishing samples

The start of the downstream migration, defined as the date by which 5% of smolts had passed through the trap, varied from late March until late April. The end of the run, after 95% of smolts had passed the trap, occurred as early as the 9th May in 2009 but as late as 20th June in 2008.

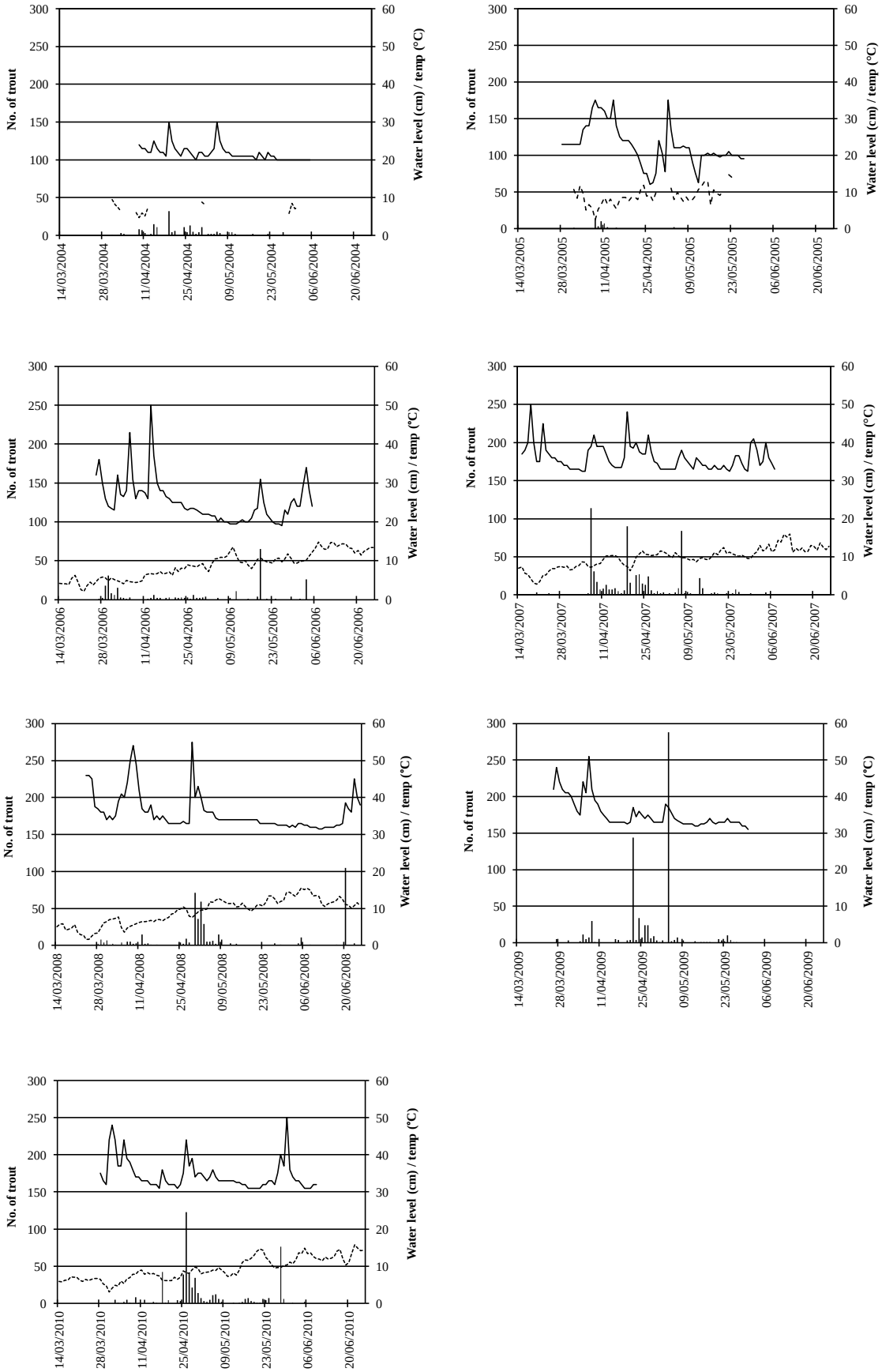


Figure 6.1: Daily catch (columns) of trout moving through the Eyrland trap in each sample year, 2004 – 2010, with water level (solid line) and water temperature (dotted line) also shown. Water temperature data incomplete for 2004.

Table 6.2: Calculation of trap efficiency for the Eyrland trap. A sub-sample of smolts were tagged and released upstream of the trap. Efficiency was calculated as the % of marked smolts recaptured as they repeated their downstream movement through the trap. This included smolts which were captured the following year. Note that the more effective Wolf trap was installed in 2007.

Year	Released upstream	Recaptured same year	Recaptured next year	Total recaptured	Trap efficiency %
2006	18	6	1	7	38.9
2007	29	12	0	12	41.4
2008	27	13	7	20	74.1
2009	28	12	8	20	71.4

The recapture rate for marked smolts released upstream of the trap is shown in Table 6.2. The measurement of trap efficiency proved problematic, as it became apparent that a number of marked smolts released upstream of the trap had remained there and "de-smolted". This only became apparent the following year when these marked trout were recaptured as smolts, termed "repeat smolts", moving downstream through the trap. In general, repeat smolts comprised S3 fish (N = 9, previously smolted as S2) with a few S2 (N = 3, previously smolted as S1). Therefore, recaptures over a single year could underestimate trap efficiency and it was necessary to include the number of smolts recaptured the following year. Efficiency of the Wolf trap operated between 2007 and 2010 ranged from 41% (2007/8) to 74% (2008/9). These should be regarded as minimum estimates as they do not account for any marked smolts that pass downstream during the summer and winter period when the trap was not in operation. Furthermore, they do not take account of mortality among the marked smolts over the year that their migration is delayed. The unreliability of these estimates is illustrated by the fact that trap efficiency did not appear to increase significantly in 2007, although the new Wolf trap installed that year clearly caught more smolts than the trap used in 2006.

6.3.2 Control of migration

The occurrence of significant daily movements of smolts in relation to absolute water level, change in water level and lunar phase are shown in Table 6.3. In each year, the largest catches of smolts generally occurred after increases in water level. Fr**o**m 2004 – 2010, there were 32 significant runs of smolt (≥5% of the total run) of which 23

occurred within 48 hours of a rise in water level. In the years when the Wolf trap was operated, 14 out of 17 significant movements of smolt were associated with an increase in water level. Significant smolt runs coincided with stable or falling water levels on eight occasions across the sampling period. Six of these occasions fell within three days of a new moon, which may have been a stimulus for downstream movement. The precise role of these factors was analysed using a general linear model, the results of which are shown in Table 6.4. These showed that water level and moon phase appeared to have some role in causing significant runs of smolts, but the nature of this role varied between sample years.

Water temperature data associated with the movement of the first smolt and the start of the main run are shown in Table 6.5. Between 2006 and 2010, the first smolts were caught in the trap when average daily water temperature was between 2.6 and 5.8°C. In 2008, when water temperature at the start of the smolt run was coldest, the main smolt run did not begin until the 25th April when the average daily temperature had risen to 9.9°C. In 2006, water temperature at the start of the smolt run was highest and the main smolt movement began earliest on 30th March when the average water temperature had actually decreased to 4.9°C. The raw temperature data recorded at the Eyrland trap are provided electronically in Appendix N.

Table 6.3: Occurrence of significant smolt runs (>5% of total run) with water level, change in water level and moon phase in the Burn of Eyrland, 2004 – 2010.

Year	Date	No. trout	% Total Run	Water level (cm)	ΔWater level, 48hrs (cm)	Days (+/-) to new moon
2004	14/04	15	8.24	25	3	-5
	15/04	11	6.04	23	3	-4
	19/04	32	17.58	30	9	0
	24/04	11	6.04	23	2	5
	26/04	13	7.14	22	-1	7
	30/04	11	6.04	22	2	11
2005	08/04	14	35	35	5	0
	09/04	3	7.5	33	2	1
	10/04	10	25	33	-2	2
	11/04	7	17.5	32	-1	3
2006	29/03	18	7.0	26	-4	0
	30/03	31	12.1	24	-2	1
	02/04	15	5.8	32	9	4
	19/05	65	25.3	31	7.5	-9
	03/06	26	10.1	34	5	6
2007	07/04	114	17.8	39	5.5	-10
	19/04	90	14.0	48	12	2
	07/05	84	13.1	38	3	-10
2008	30/04	71	15.6	40	22	-5
	01/05	36	7.9	43	3	-4
	02/05	59	12.9	40	3	-3
	03/05	29	6.4	36.5	-3.5	-2
	20/06	105	23.0	38.5	4.5	-14
2009	22/04	144	21.3	37	4	-3
	24/04	34	5.0	36	-2.5	-1
	04/05	288	42.7	37	5	9
2010	18/04	42	7.9	36	5	4
	25/04	39	7.4	35	4	11
	26/04	123	23.2	44	9	12
	27/04	40	7.5	37	9	13
	29/04	34	6.4	34	-5	15
	28/05	76	14.3	40	5	14

Table 6.4: Analysis of the role of different environmental factors in causing significant downstream movements of smolts using a general linear model. Factors analysed included absolute daily water level, change in water level (within 48hrs) and lunar phase (days before or after the new moon).

Source	DF	Adj SS Value	Adj MS	F-Value	P
level	1	1.811	1.8107	7.84	0.012
level*Year	6	8.986	1.4977	6.48	0.001
days to moon*Year	6	3.133	0.5222	2.26	0.084
Error	18	4.158	0.2310		
Total	31	32.056			

Table 6.5: Water temperature recorded at capture of first smolt and at start of main smolt run in the Burn of Eyrland, 2006 – 2010. Water temperature data was recorded using a Gemini Data Loggers (TinyTag Plus) installed by the Eyrland trap.

	1st smolt		After 5% of smolts	
Year*	**Date**	**Average daily temp. (°C)**	**Date**	**Average daily temp. °C)**
2006	28/3	5.8	30/3	4.9
2007	19/3	3.1	7/4	7.2
2008	26/3	2.6	25/4	9.9
2009	27/3	-	8/4	-
2010	2/4	4.8	18/4	6.2

* Detailed water temperature data were not available for 2004, 2005 & 2009.

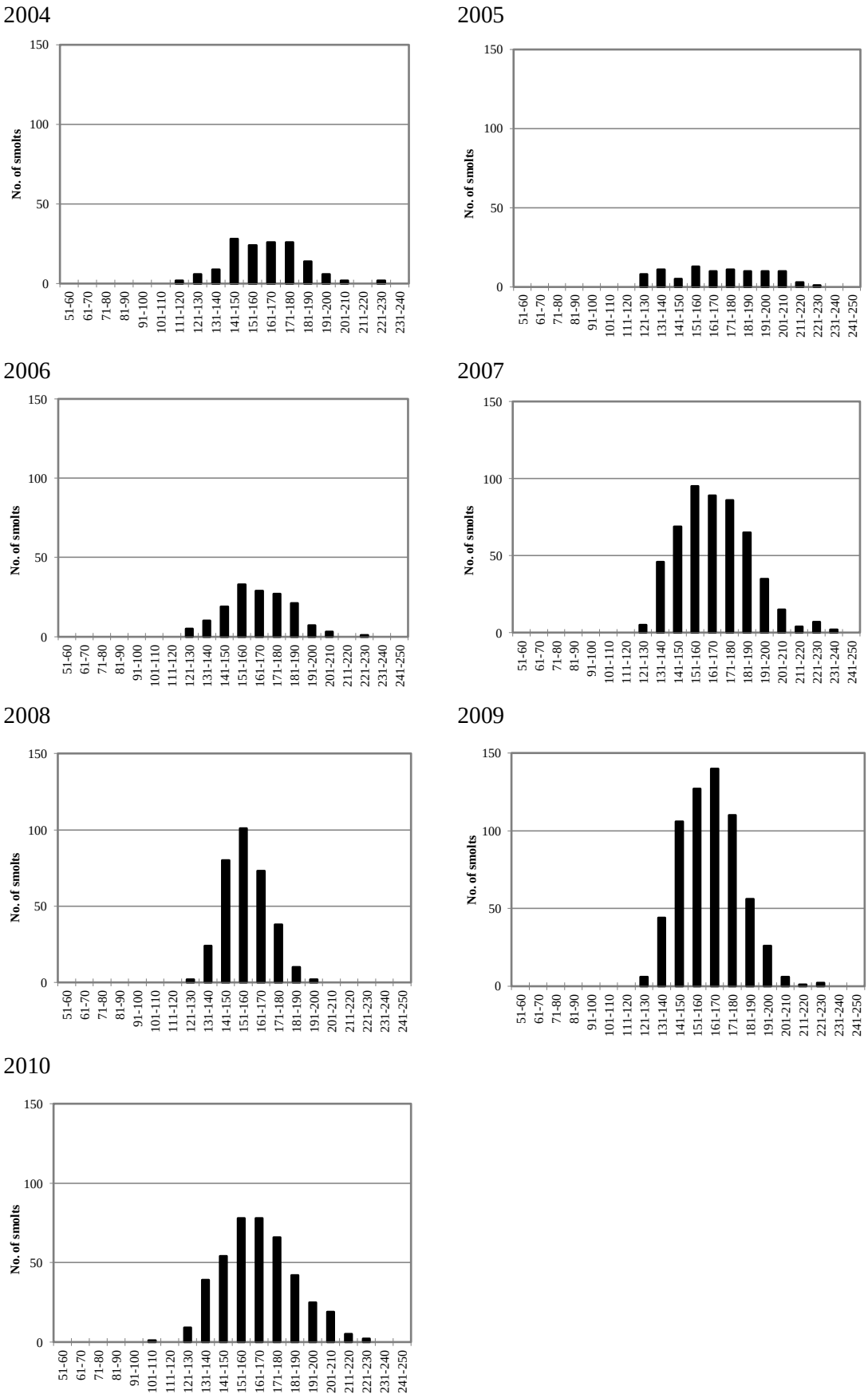


Figure 6.2: Length (fork length) frequency distributions of annual smolt catches from the Burn of Eyrland trap, 2004 - 2010. Length cohorts (10mm increments) are shown along the x-axis. Non-smolting trout excluded from the analysis.

6.3.3 Smolt size and age structure

The oMFL of all individual smolts over the sampling period (N = 2284) was 163.8 ± 0.4mm. Between years, oMFL varied between 157.1 ± 0.7mm and 169.3 ± 2.9mm (Table 6.). The smallest individual smolt recorded was 101mm and the largest was 233mm. Each year's sample comprised S1, S2 and S3 smolts and the MSA varied between 1.7 years in 2004 to 2.1 years in 2010. Overall MSA was 1.9 ± 0.01 years. S2 smolts were the most common and represented between 59.0% and 92.8% of each year's sample. S1 smolts represented between 1.0% and 27.6%. The proportion of S3 smolts was usually less than 10% but increased to 23.6% in 2010. Despite the occurrence of three age cohorts, length frequency analysis showed a uni-modal distribution in each year (Figure 6.2), which reflected the overlapping length range for each age cohort. oMFL for each age cohort is shown in Figure . In general, size increased with age although in 2008 there was little difference in size between the three cohorts.

In each year, the mean size and age of smolts caught in the trap decreased through the spring period. The oMFL of smolts caught in 15/16 days periods through the spring is shown in Figure . When smolt migration was delayed by low water conditions in 2005 and 2008, the decline in mean smolt size levelled off and in 2008, when a large number of smolts were held back until late June, their mean size had increased relative to those migrating in late May. S1 smolts tended to migrate later in spring relative to old cohorts. In five of the six years that data were available (2005 was excluded), S1 smolts migrated significantly later in spring than S2 and S3 smolts (Table 6.7). Overall the six years of data, the mean migration date of S1 smolts was between 7 and 28 days later than the older cohorts, with a median delay of 15 days.

6.3.4 Freshwater growth

Growth curves constructed by back calculation for S1, S2 and S3 smolts, averaged over the sampling period 2004 – 2010, are shown in Figure. Mean annual growth increments for each age cohort are provided in Table S1 smolts exhibited the fastest growth in freshwater, followed by S2 smolts, which in turn were faster growing than S3 smolts. In S2 smolts, the second year's growth exceeded the first while S3 smolts also showed a slight acceleration in mean growth between successive years.

Table 6.6: Annual size and age data for smolts sampled in the Eyrland trap, 2004 – 2010.

Year	No. smolts	oMFL ±se (mm)	Min (mm)	Max (mm)	MSA (yrs)	S1		S2		S3	
						%	oMFL ± se (mm)	%	oMFL ± se (mm)	%	oMFL ± se (mm)
2004	148	162.4 ± 1.7	115	223	1.8 ± 0.04	27.6	143.3 ± 1.9	68.3	168.5 ± 1.7	4.1	188.5 ± 8.1
2005*	92	169.3 ± 2.9	121	215	1.9 ± 0.05	17.4	132.2 ± 2.0	79.3	175.9 ± 2.7	3.3	205.7 ± 7.9
2006	155	164.6 ± 1.5	124	222	2.0 ± 0.03	9.4	143.2 ± 3.1	81.9	166.0 ± 1.5	8.7	173.2 ± 5.6
2007	519	166.6 ± 0.9	126	233	1.9 ± 0.02	20.2	144.0 ± 1.0	74.1	169.3 ± 1.7	5.8	185.8 ± 2.2
2008	333	157.1 ± 0.7	125	193	2.0 ± 0.03	4.5	151.6 ± 3.6	91.9	159.4 ± 1.4	3.6	162.3 ± 3.4
2009	624	163.0 ± 0.7	124	225	2.0 ± 0.02	1.0	146.0 ± 12.7	92.8	164.6 ± 1.3	6.2	191.8 ± 5.1
2010	420	165.6 ± 1.0	101	222	2.1 ± 0.05	17.4	138.9 ± 1.9	59.0	166.5 ± 2.1	23.6	184.0 ± 3.6

Table 6.7: Mean migration date for S1, S2 and S3 smolts caught in the Burn of Eyrland trap, 2004 - 2010. Average migration date was taken as the average of all dates on which smolts of each age passed through the trap. One-way ANOVA used to determine significance of differing migration dates between age cohorts.

Year	Average migration date for each smolt age			ANOVA result	Significant differences in migration date between age cohorts (“>” = later than)
	S1	S2	S3		
2004	2/5/04	19/4/04	19/4/04	$F(2, 117) = 17.90$, $p < 0.001$	S1 > S2, S3
2006	22/5/06	11/5/06	24/4/06	$F(2, 126) = 4.96$, $p = 0.008$	S1, S2 > S3
2007	7/5/07	18/4/07	17/4/07	$F(2, 445) = 105.35$, $p < 0.001$	S1 > S2, S3
2008	10/6/08	8/5/08	16/5/08	$F(2, 93) = 4.30$, $p = 0.016$	S1 > S2, S1 = S3, S2 = S3
2009	23/5/09	27/4/09	15/4/09	$F(1, 189) = 7.18$, $p = 0.001$	S1 > S2 > S3
2010	15/5/10	1/5/10	21/4/10	$F(2, 148) = 16.83$, $p < 0.001$	S1 > S2, S3

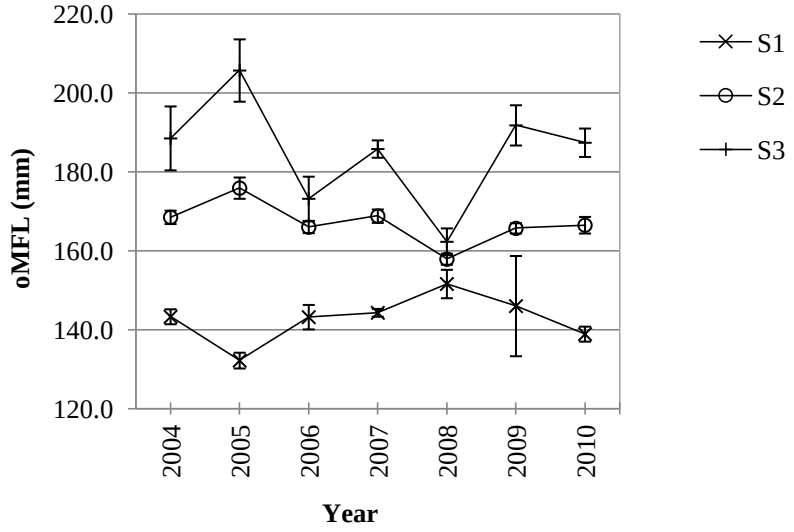


Figure 6.3: Comparison of annual oMFL ± se (mm) in S1, S2 and S3 smolts sampled from the Burn of Eyrland, 2004 - 2010.

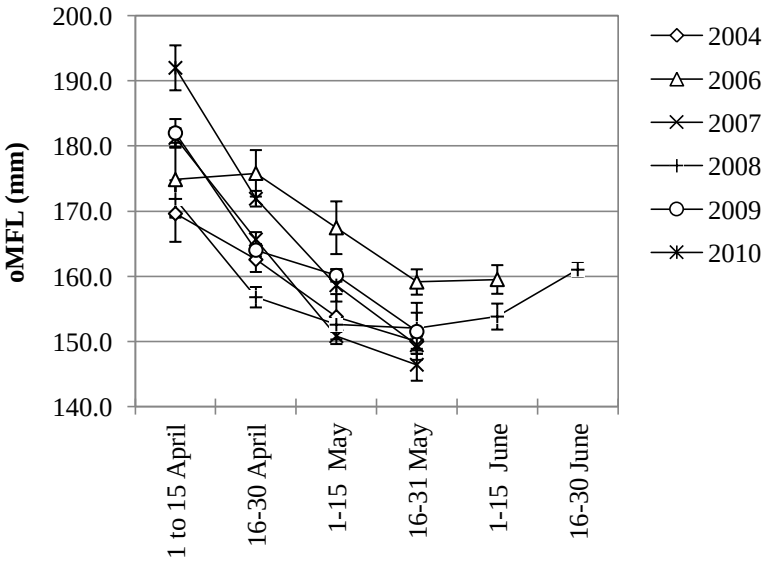


Figure 6.4: Variation in oMFL ± se (mm) of smolts (all ages) caught at regular intervals through the spring period at the Eyrland trap, 2004 – 2010 (2005 excluded due to ineffective trap).

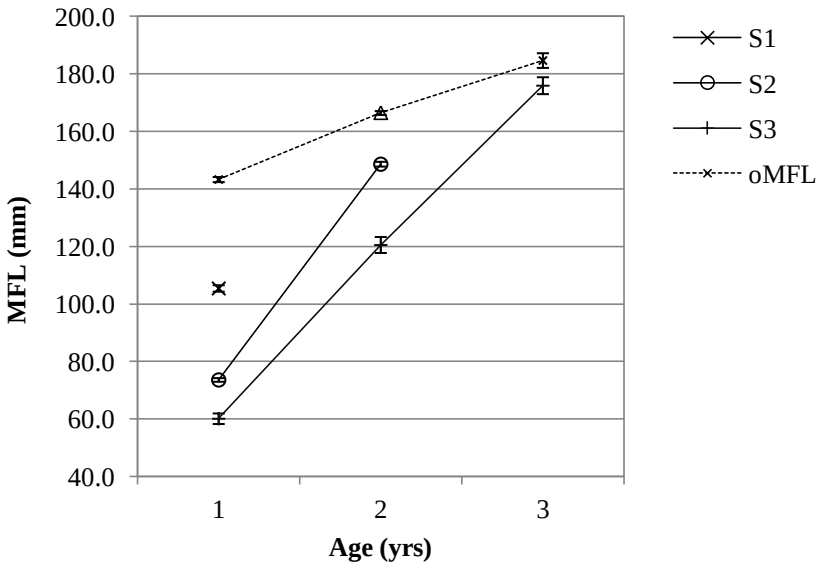


Figure 6.5: Back calculated growth curves for one, two and three year old smolts migrating from the Burn of Eyrland, 2004 – 2010. Dotted line represents the oMFL of each age cohort at sampling, i.e. including B growth.

Analysis of individual data in specific sample years showed that in general, annual growth increments were directly related to ultimate smolt size. For example, in S2 smolts, there was a direct relationship between each of the first and second year growth increments and size at smolting (both cFL and oFL). However, there were some exceptions to this rule. For example, in S1 smolts, first year growth, *i.e.* size at end of winter, was directly related to the size at seawater entry in 2010 but not in 2007. In S3 smolts sampled in 2007, first year growth was related to cFL and oFL. However, in S3 smolts sampled in 2010, 3rd year growth was not related to either cFL or oFL (it was in 2007). These relationships are shown in Table 6.9.

Table 6.8: Mean annual growth increments in S1, S2 and S3 smolts sampled from the Eyrland burn, 2004 – 2010. Size at end of winter before migration (cMFL) and at seawater entry (oMFL) is also shown for each age cohort.

Smolt age (yrs)	Mean annual growth increment (mm)			cMFL (mm)	oMFL (mm)
	1st yr	2nd yr	3rd yr		
1	107.0	-	-	107.0	144.5
2	70.9	77.8	-	148.7	166.3
3	55.0	57.4	59.3	171.5	182.6

Table 6.9: Results of regression analysis of relationship between annual growth increments and size at smolting for individual smolts within sample years. Note that cFL = size at end of winter before smolting and oFL = size at sampling. Non-significant relationships are highlighted with a "". P-values are bonferroni adjusted where multiple tests are performed on the same data.*

Cohort	Comparison	df	R	P
S1, 2007	1st VS oFL	87	+0.164	0.257*
S1, 2010	1st VS oFL	32	+0.490	0.009
S2, 2007	1st VS cFL	334	+0.685	<0.001
	1st VS oFL	334	+0.623	<0.001
	2nd VS cFL	334	+0.651	<0.001
	2nd VS oFL	334	+0.426	<0.001
S2, 2008	1st VS cFL	88	+0.721	<0.001
	1st VS oFL	88	+0.424	<0.001
	2nd VS cFL	88	+0.478	<0.001
	2nd VS oFL	88	+0.398	<0.001
S2, 2009	1st VS cFL	178	+0.754	<0.001
	1st VS oFL	178	+0.683	<0.001
	2nd VS cFL	178	+0.663	<0.001
	2nd VS oFL	178	+0.628	<0.001
S2, 2010	1st VS cFL	85	+0.733	<0.001
	1st VS oFL	85	+0.782	<0.001
	2nd VS cFL	85	+0.712	<0.001
	2nd VS oFL	85	+0.496	<0.001
S3, 2007	1st VS cFL	26	+0.465	0.033
	1st VS oFL	26	+0.368	0.129*
	2nd VS cFL	26	+0.779	<0.001
	2nd VS oFL	26	+0.762	<0.001
	3rd VS cFL	26	+0.406	0.079*
	3rd VS oFL	26	+0.403	0.082*
S3, 2010	1st VS cFL	34	+0.636	<0.001
	1st VS oFL	34	+0.681	<0.001
	2nd VS cFL	34	+0.738	<0.001
	2nd VS oFL	34	+0.664	<0.001
	3rd VS cFL	34	+0.207	0.483*
	3rd VS oFL	34	+0.155	0.764*

Table 6.10: Freshwater growth in trout which had de-smolted and spent an additional year in the burn before smolting again the following year, Eyrland burn, 2007 – 2010. Figures in brackets indicate the equivalent sizes of S2 and S3 smolts (overall) sampled from the Eyrland burn.

Age cohort	N	MFL (mm) at age		
		1.	2.	3.
S2	3	103.7 (70.9)	174.1 (148.7)	-
S3	9	68.3 (55.0)	131.9 (112.4)	196.0 (171.6)

Smolts which de-smolted and remained for an additional year in freshwater appeared to maintain growth rates comparable to that in previous years (Table 6.10). Repeat S2 smolts (initially smolted as S1s) were significantly larger than the general mean for S2 smolts ($F(1,686) = 4.08$, $p = 0.044$), although this was based on a sample of only three individuals. Repeat S3 smolts (initially smolted as S2s) were slightly more numerous ($N = 9$) and were also significantly larger at smolting than the general mean for S3 smolts ($F(1,83) = 5.26$, $p = 0.024$).

6.3.5 B-growth

B-growth among smolts was observed frequently and its expression varied between different aged smolts. Average B-growth over the entire sampling period, in terms of length and weight increase, was highest in S1 smolts and least in S3 smolts (Table 6.11). As S1 smolts were smallest at the end of the winter prior to migration, the impact of B-growth was to increase their size significantly and to narrow the difference in mean size between the three age cohorts from 64.6mm at the end of winter to 38.1mm at the point of seawater entry. The length-weight relationship in smolts from the Eyrland burn is shown in Appendix T.

Table 6.11: Average B-growth observed in one, two and three year old smolts sampled from the Burn of Eyrland, 2007 – 2010. Weight data is calculated from the length-weight relationship derived from 2007 smolt data, $y = 0.0036x2 - 0.4339x + 17.825$, where y = weight (g) and x = fork length (mm).

Age	cMFL ± se (mm)	oMFL ± se (mm)	B-growth ± se (mm)	B-growth ± se (g)
S1	105.5 ± 1.1	143.3 ± 1.3	37.9 ± 0.9	17.1 ± 0.6
S2	148.7 ± 0.8	166.5 ± 0.7	17.8 ± 0.5	12.3 ± 0.3
S3	176.0 ± 2.9	184.7 ± 2.6	8.6 ± 1.1	9.3 ± 0.9

Effect of smolt size

Mean B-growth in same aged smolts between sample years varied inversely with smolt size at the end of winter before migration ($p<0.05$ for each age cohort). For example, in years when the cMFL of S2 smolts was small at the end of winter, a larger amount of plus growth was achieved prior to migration compared to years when the cMFL at the end of winter was larger. This trend is illustrated in Figure 6.6 for S1, S2 and S3 smolts.

Individual B-growth showed a similar trend within sample years although the strength of the relationship varied between ages and also between years. In 2007 and 2010 all three smolt age cohorts were well represented. In each age cohort in both years there was a highly significant inverse relationship between individual size at the end of winter (cFL) and the amount of B-growth achieved by the point of seawater entry (Table 6.12). On average, less B-growth was exhibited by each age cohort in 2010 than in 2007. This is quantified in Table 6.13 and illustrated in Figure 6.7. This may have been the result of colder spring temperatures in 2010. The relationship between mean annual B-growth and spring temperature data is analysed below.

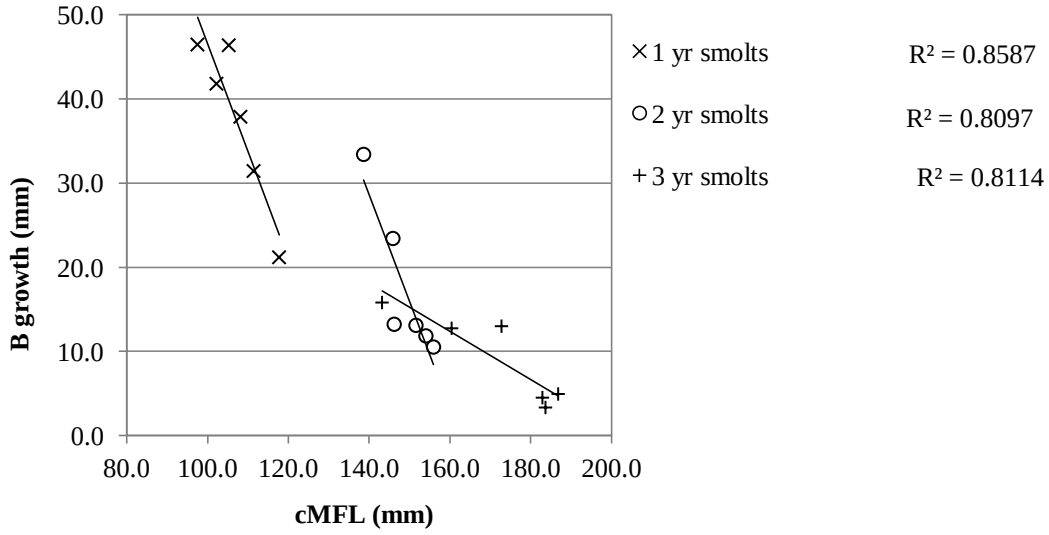


Figure 6.6: Relationship between mean fork length at the end of the last winter before migration and the extent of B-growth achieved subsequently in S1, S2 and S3 smolts sampled from the Burn of Eyrland, 2004 – 2010.

Table 6.12: Regression analysis of the relationship between size at end of the winter before migration and B-growth in S1, S2 and S3 smolts sampled from the Eyrland burn in 2007 and 2010.

Year	Smolt age (yrs)	df	R	P
2007	1	89	0.714	p<0.001
	2	332	0.615	p<0.001
	3	24	0.364	p<0.05
2010	1	29	0.706	p<0.001
	2	81	0.540	p<0.001
	3	32	0.514	p<0.001

Table 6.13: Mean B-growth expressed as the increase in length (mm) and weight (g) achieved by S1, S2 and S3 *smolts sampled from the Eyrland burn in 2007 and 2010. The length-weight relationship is derived from Eyrland smolts sampled in 2007 and is described as* $y = 0.0036x^2 - 0.4339x + 17.825$, *y = weight (g) and x = fork length (mm).*

Smolt age (yrs)	Mean B-growth (mm)		Mean B-growth (g)	
	2007	2010	2007	2010
1	42.0	26.0	19.0	11.0
2	23.4	10.5	16.4	7.7
3	13.0	4.5	11.1	4.0

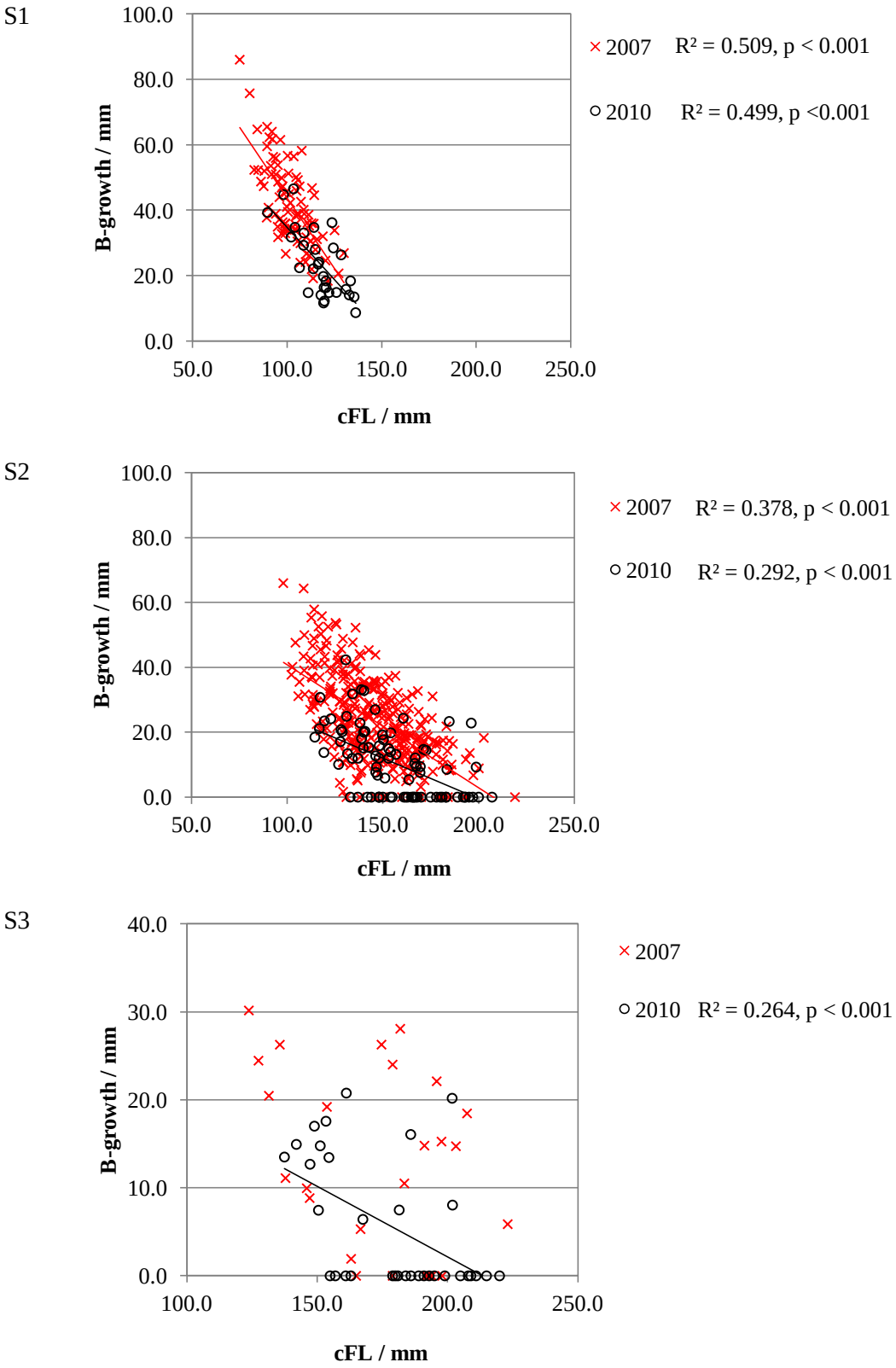


Figure 6.7: Relationship in individual S1, S2 and S3 smolts between FL at end of winter and amount of B-growth achieved by the time of sampling in 2007 (S1, N = 89, S2, N = 332, S3 N = 24) and 2010 (S1, N = 29; S2, N = 81; S3 N = 32).

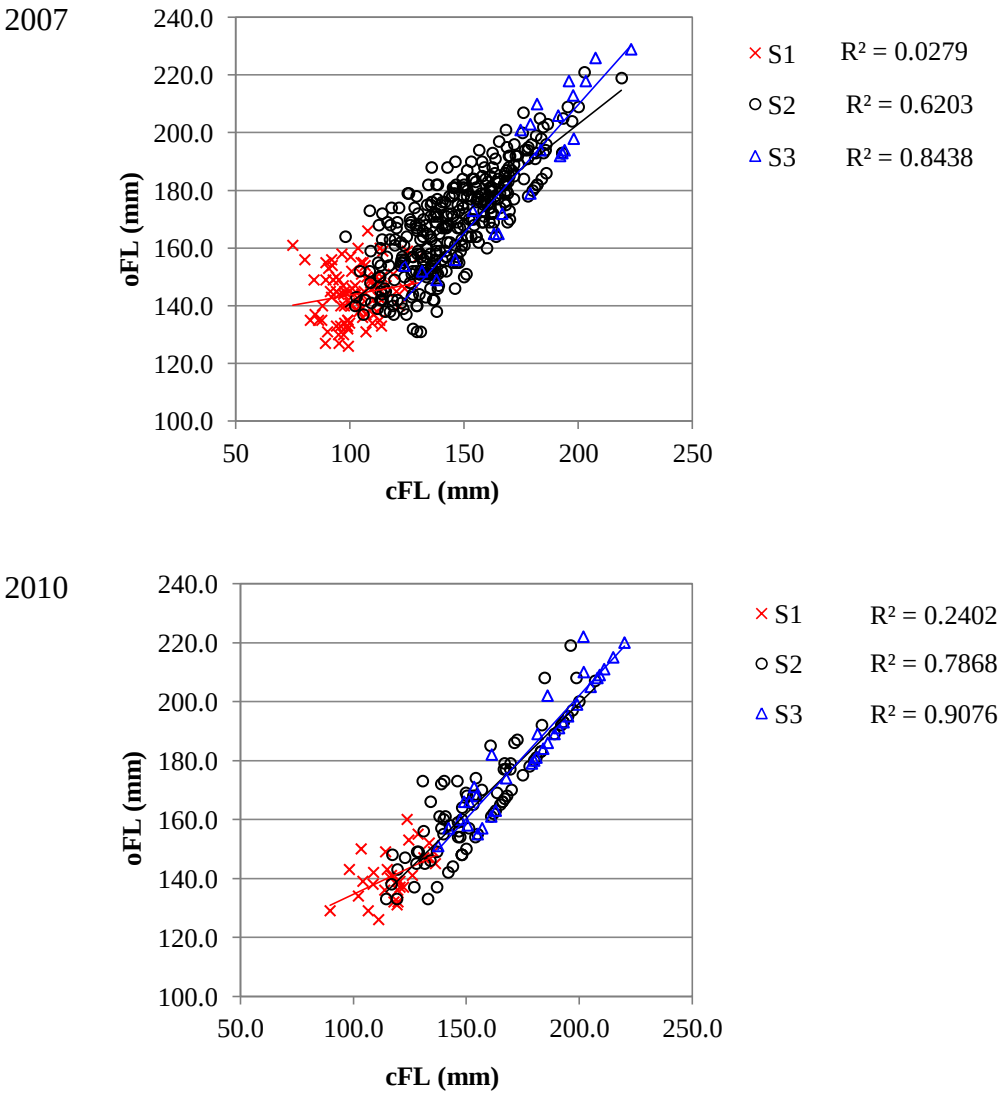


Figure 6.8: Relationship between size at end of winter (cFL) and at seawater entry (oFL) in S1, S2 and S3 smolts sampled from the Eyrland burn in 2007 (S1, N = 88, S2, N = 334, S3 N = 26) and 2010 (S1, N = 31, S2, N = 83, S3 N = 34).

Analysis of individual data also showed a strong direct relationship between smolt size at end of winter and at the point of seawater entry, *i.e.* before and after the occurrence of B-growth, in S2 and S3 smolts, as might be expected. However, in S1 smolts, this relationship was present in 2010 ($df = 33$, $R = 0.490$, $p<0.001$) but not in 2007 ($df = 87$, $R = 0.529$, $p = 0.126$). This suggested that the size of S1 smolts at seawater entry could in some years be determined by the extent of B-growth achieved prior to migration rather than by their size at the end of winter. These relationships are illustrated in Figure 6.8.

Effect of temperature

Between years, the expression of B-growth increased directly with the extent of the spring growing period, defined as the number of days between February and May (inclusive) where air temperature exceeded 5.6 °C. Regression analysis showed that this relationship was significant in each age cohort of smolts (S1: df = 170, R = 0.542, $p < 0.001$; S2: df = 879, R = 0.298, $p < 0.001$; S3: df = 85, R = 0.360, $p < 0.001$). These relationships are shown in Figure 6.9. Spring temperature regimes in 2007 (110 days) and 2010 (91 days) were at opposite ends of the range in spring growing conditions measured over the sampling period. This links in with the earlier observation that B-growth across all age cohorts was on average, less in 2010 than it was in 2007.

An additional trend that may be linked to temperature difference between years was the temporal expression of B-growth through the spring migration period. Although B-growth was generally not observed on smolts passing through the trap until mid to late April, the extent of B-growth did not always increase thereafter. For example, in S1 smolts, which showed the greatest B-growth, there was a direct relationship between B-growth and date in 2010 (df = 30, R = 0.549, p = 0.001), when there was a colder spring (91 growing days), but none in 2007 (df = 87, R = 0.046, p = 0.672) when there was a warmer spring (110 growing days). These trends are illustrated in Figure 6.10.

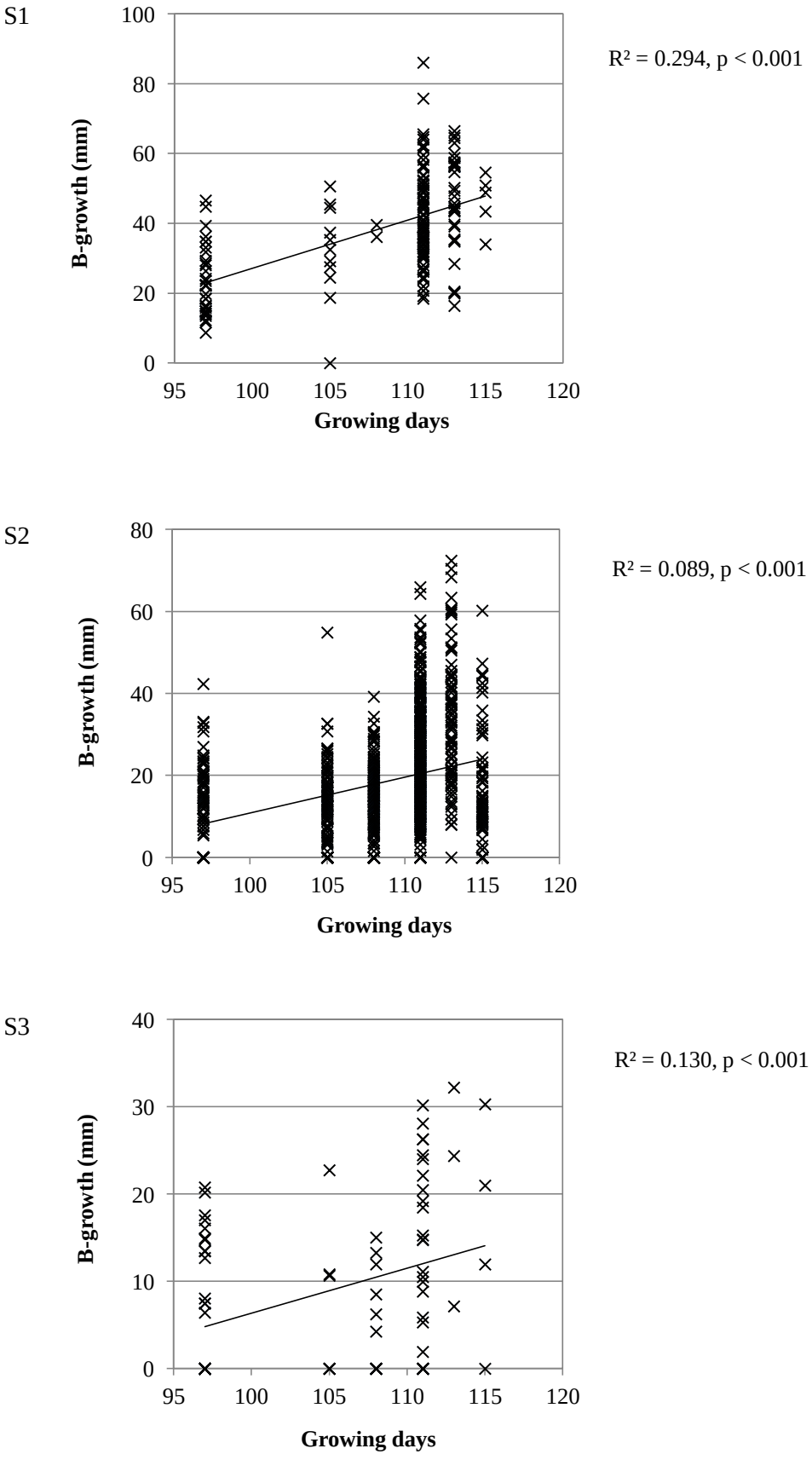


Figure 6.9: Relationship between the extent of the spring growing period in terms of air temperature (number of days where air temp exceeds 5.6°C between February & May, inclusive) and B-growth attained in S1, S2 and S3 smolts from the Eyrland burn, 2004 - 2010.

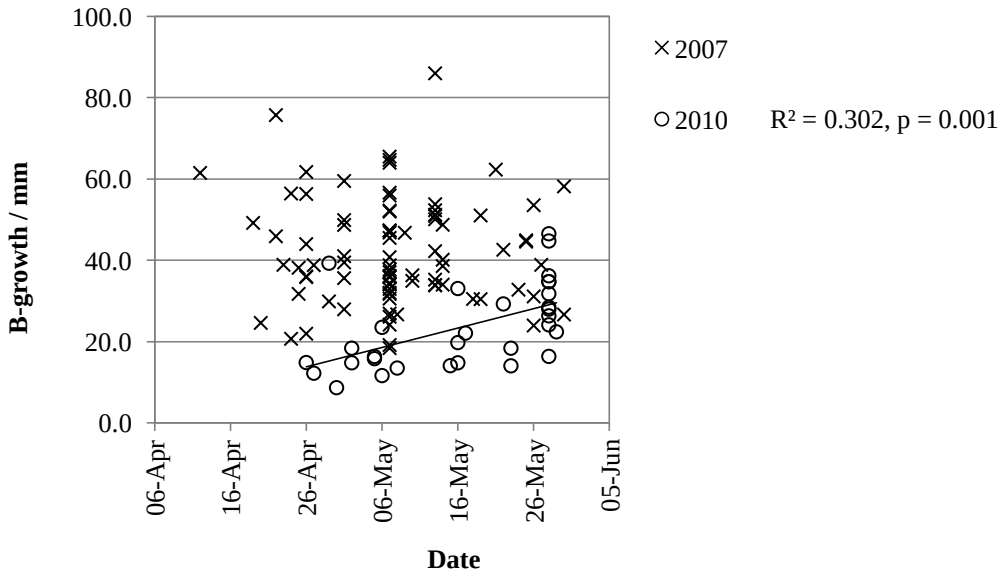


Figure 6.10: Relationship between the extent of B-growth expressed by individual S1 smolts and date of capture in the spring migration period, 2007 & 2010.

6.3.6 Target size for smolting

A target size for smolting was set at 130mm, the length at which 95% of S1 smolts met or exceeded at the point of sampling (including B-growth). The growth performance of each age cohort of smolts in relation to this target is presented in Table 6.14.

Table 6.14: Number of smolts from each age cohort which were ≥130mm when sampled from the Eyrland burn, 2007 – 2010.

Smolt Age	N	Age (yrs) & no. fish ≥130mm (%)		
		1	2	3
S1	123	117 (95.1)	-	-
S2	685	1 (0.1)	681 (99.4)	-
S3	76	0 (0.0)	24 (31.6)	76 (100)

At seawater entry the mean size (oMFL) of S1 smolts sampled between 2007 and 2010 (N = 123) was 142.1mm although individuals ranged in size from 101mm to 166mm. However, over 95% of S1 smolts sampled were 130mm or greater in size, at the point of seawater entry (oFL). The mean size of S2 and S3 smolts one year prior to migration was 73.7mm and 120.6mm, respectively. Analysis of individual data for S2 smolts showed that only one out of 685 exceeded 130mm at age one. However, among S3s, approximately 32% (24/76) smolts exceeded 130mm at age two.

6.4 Discussion

This chapter contains detailed smolt data from the Eyrland burn collected over a seven year period and the analysis of freshwater growth dynamics in relation to migratory behaviour is novel in a Scottish context. The main findings highlight the possible role of the new moon as a stimulus to downstream movement during stable or falling water levels and the first ever documentation of wild sea trout smolts de-smolting in one year and re-smolting the following year. It was also found that B-growth in freshwater after the end of winter significantly increased smolt size by the point of seawater entry. The greatest B-growth was observed in the youngest (and smallest) smolts, which allowed them to catch up in size with larger older smolts by the time of seawater entry. Moreover, an inverse relationship between size at end of winter and B-growth was present within age cohorts. A temperature effect on mean B-growth was observed between years. These trends reopen the debate concerning the presence of a threshold size in sea trout smolts.

Total catch and productivity

From 2007 to 2010, when the Wolf trap was operating, the annual smolt catch ranged from 333 to 624. These should be taken as minimum estimates, as it was unlikely that the trap was operating with 100% efficiency. However, attempts to measure trap efficiency using traditional methods were clearly affected by a tendency for some of the marked smolts released upstream to de-smolt and remain in freshwater. This phenomenon is discussed in greater detail below. Estimates of trap efficiency based on same year recaptures did not exceed 50%. While the estimated efficiency for 2008 and 2009 rose to around 70% when recaptures made the following year were added to the total, the estimate for 2007 remained at around 40%. Moreover, having to measure efficiency over a two year period introduces large scope for error. As the trap was only operated during the spring period, it is possible that some of the marked smolts moved downstream after the trap was removed, usually in late May or June until the following year. It is also possible that some of the marked smolts died in the intervening period. Finally, it is possible that surviving smolts simply remained in the burn as resident trout. Given these unknowns, it is clear that the available efficiency estimates should be treated with caution if used to infer total smolt production. In this light a cautious

approach might be to simply treat the actual annual catches as minimum estimates until further information becomes available.

Annual, unadjusted catches equated to a productivity of between 2.7 and 5 smolts/100m^2 of wet area in the Eyrland burn. This represents the first documented effort in Scotland to quantify the production of sea trout smolts in a system that does not also support Atlantic salmon. The only other Scottish estimate of trout smolt production relates to two tributaries of the River Spey, which also support Atlantic salmon. Rates of trout production there were calculated based on rotary screw trap surveys for the rivers Truim and Tromie and were found to be approximately 0.6 and 2.0 smolts/100m^2 (Laughton, 2010a & 2010b). Production of Atlantic salmon in each river was approximately 4.0 smolts/100m^2. Other unpublished estimates for sea trout smolt production exist from studies elsewhere, *e.g.* the Shieldaig, Tournaig and the North Esk. Published estimates of smolt production are available outside Scotland. In the Burishoole system in Ireland, sea trout smolt production was reported to be approximately 4 smolts per hectare, or 0.04 smolts/100m^2 (Matthews *et al*., 1997). What seems a very low rate is almost certainly due to the fact that the area of lacustrine habitat was added to the area of stream and river habitat to arrive at that estimate. The Burishoole also supports a sympatric population of Atlantic salmon, which dominates in terms of smolt production. Hesthegan *et al.* (1986) reported a higher value of 1.2 smolts/100m^2 for sea trout in a small Norwegian river again dominated by Atlantic salmon. The River Bresle in northern France also supports sympatric trout and salmon populations but trout dominates smolt output numerically. In that case, the long-term average rate of smolt production was estimated at 2.6 smolts/100m^2 (Euzenat *et al*., 2006). Denmark provides two examples of which are perhaps most similar in context to the Eyrland system, *i.e.* small systems which support anadromous brown trout only. Mortensen (1977) estimated smolt output of approximately 4 per 100m^2 in the Bisballe Baek, a stream of only 450m in length, which flows into Lake Hald. However, although the author termed emigrating fish as "smolts" it was apparent that they were emigrating to the lake and were not in fact smolts in an anadromous sense. Rasmussen (2006) estimated a general figure of smolt production in Denmark generally of between 15 and 20 smolts per 100m^2, although many systems in Denmark have been artificially stocked. These examples demonstrate the difficulty in finding a "like for like" comparison but also highlight the value of the Eyrland data.

According to the examples mentioned above, stream size does not seem to have an obvious effect on the rate of smolt production. However, from a study of 167 rivers in south-west Sweden, Bohlin *et al.* (2001) reported that the rate of anadromy in brown trout populations declined with altitude and hypothesized that this was due to the increasing "cost" of migration. This fits with observations on the River Spey that the production of Atlantic salmon smolts is depressed in higher altitude tributaries (Laughton *et al*., 2008a). In addition to the greater "costs", other factors may combine to affect productivity in high altitude catchments such as decreased water temperature, habitat and food availability. However, as so few estimates exist in the literature it is difficult to draw any firm conclusions on this.

De/re smoltification

The tendency for some sea trout smolts to de-smolt one year and subsequently re-smolt the next year was a notable phenomenon that has not been reported before in any anadromous salmonid in the wild[1] and highlights the inherent flexibility in the brown trout life cycle. In wild Atlantic salmon, smolting in juveniles is described as a "once in a lifetime event" and desmoltification involves the loss of the "preparatory adaptations" for the transition between freshwater and saltwater, such as the loss of hypo-osmoregulatory ability (Björnsson & Bradley, 2007; Stefansson *et al*., 2008). Desmoltification is stimulated by decreasing photoperiod and by high or increasing freshwater temperatures (Soivio *et al*., 1988; Kurokawa, 1990). Delays in downstream migration may increase the risk of desmolting. Stefansson *et al*. (2003) reported that dams can cause both delays and direct mortality in salmon smolts. It could reasonably be assumed that a similar mechanism may affect sea trout. In this study, the presence of the dam (on which the Eyrland trap was installed) undoubtedly checked the progress of smolts on their way downstream, particularly during periods of low flow, and may have encouraged de-smolting among some fish, *e.g.* in 2008. However in 2009, water levels were much more consistent during the spring, yet desmolting still occurred, evidenced by the recapture of marked smolts in 2010. Other potential factors to consider include the experience of being trapped and handled during the processing phase. Handling is known to result in a stress response in salmonids and it has been reported that a minimum period of two weeks is required for stressed fish to fully recover (Pickering *et al*., 1982). In a stocking experiment, elevated stress caused by handling and transport of

[1] It has been experimentally demonstrated in Atlantic salmon (Eriksson, 1984; Shrimpton *et al*., 2000).

hatchery reared Atlantic salmon smolts was thought to have contributed to poor catch returns (Iversen *et al*., 1998). In a recapture experiment on the Miramichi River, New Brunswick, the rate of survival of wild Atlantic salmon smolt to the adult stage was much higher than in tagged or fin-clipped smolts (Saunders & Allen, 1967). The evidence suggests therefore that the dam on the Eyrland burn coupled with the exposure to trapping and handling, could have contributed to the observed desmolting process.

The total number of delayed smolts did not exceed 2% of the total smolt catch but this would not account for any smolts that died in the year after desmolting or any smolts which desmolted without being captured. Growth data for trout which de-smolted and remained in freshwater showed that they achieved reasonable growth in the year following their failed migration. This has not previously been documented. This result suggests that growth conditions in the burn were not limiting and also that appetite in desmolted fish was not affected by their failure to migrate to sea. Their determination to adopt a migratory strategy, evidenced by their capture as smolts the following spring also suggests that genetics play a major role in controlling migratory behaviour, although the performance of these delayed smolts at sea and on return to breed remains unknown. Stefansson *et al.* (2008) described reduced marine growth performance in smolts that have been delayed in their migration to sea.

Control of downstream migration

Water level and lunar phase influenced the downstream movement of smolts, but the strength of this influence varied between years. However, the presence of the dam beside which the smolt trap was located may also have influenced movement of smolts. It was clear that smolts accumulated upstream of the dam and would pass downstream when water levels rose. However this also suggests that they were moving downstream in conditions that were different from those required to navigate a dam, *i.e.* an increase in water level. The effect of the dam therefore was to cause large single movements of smolts when water levels increased sufficiently. It is perhaps unsurprising therefore that a correlation between daily smolt catch and water level increase was observed, but it is important to appreciate that the presence of the dam probably contributed to the strength of the correlation. Other more subtle controls governing the migration of smolts prior to reaching the dam may therefore be overlooked. Unfortunately, the methods required to examine these were not available to the author.

The fact that the extent of water level increase was not proportional to the size of the associated catch was not surprising as other factors are likely to be involved. For example, the size of the catch may depend on how long it has been since the last increase in water level or on the number of smolts remaining to pass (*ibid*). The occurrence of significant smolt movements at times when water level was steady or falling was interesting. It was noted that 75% of these events occurred within 3 days of a new moon although further statistical analysis showed that the association between smolt movements and lunar phase varied between years. Lunar phase has been reported to influence hormonal levels in salmonids during the smoltification process (Grau *et al.*, 1981) and the downstream migration of chinook salmon (*Onchorhynchus tshawytscha*) smolts has been observed to coincide with new or waning moon phases (Roper & Scarnecchia, 1999). The benefits of moving downstream during a new moon period would be greater darkness to avoid predation and the occurrence of spring tides, which may assist the seaward passage of smolts particularly in small systems like the Eyrland burn where there is a very sharp transition between freshwater and the sea. Byrne *et al*. (2004) rejected lunar phase as an influence on brown trout smolt movements in the Burrishoole system. However that system is much larger and also contains several loughs that might cause smolts to pause or be delayed during their downstream migration. Therefore, the conditions that encourage smolt movements in upper parts of the catchment may not still exist by the time they reach the lower part of the catchment where they were trapped. It could be argued that subtle controls on migration are more evident in small systems, where smolt runs initiated anywhere in the system will shortly arrive in the lower reaches while the conditions which initiated those runs are still detectable, *e.g.* new moon periods.

Water temperature appeared to play a role in initiating the start of the migration in each year. It was apparent that in colder years, the main movement of smolts occurred later in the spring and *vice versa*. This suggests that water temperature has a greater influence than photoperiod. The first smolts were caught when average daily water temperature was between 2.6 and 5.8°C. However, the main run (discounting the first 5%) occurred when water temperatures were warmer, between approximately 5 and 10°C. This was similar to that measured by Byrne *et al*. (2004), who found main runs occurring at temperatures of between 5 - 9°C with a mean of 6.6°C.

Smolt size and age

Smolts from the Eyrland burn were a little smaller and younger on average than other Scottish populations studied recently (Table 6.4). In fact, smolt age in the Eyrland burn is the youngest of the examples given and in a Scottish context do not follow the general trend that smolt age increases with latitude as commonly reported (Jonsson & L'Abée-Lund, 1993). In fact the Eyrland data turned this relationship on its head, exhibiting the youngest MSA (1.7yrs) of any documented sea trout population in Scotland (apart from in the Bu, another Orkney burn, see Chapter 5). The trend reported by Jonsson & L'Abée-Lund (1993) was seen in 102 European rivers at latitudes of between 54° and 70° north. If the data from Scottish populations (based almost completely on the work of G.H. Nall in the 1930s) and others at similar latitude (54° to 59° north) are considered in isolation, one could argue that no trend existed between smolt age and latitude, but becomes evident over a wider north-south distribution. It is possible that Scotland does not experience a sufficient range in temperatures, or a smooth temperature gradient, to cause noticeable differences in smolt age between northern and southern populations. In a Scottish context, Orkney has a relatively mild climate, owing to its maritime situation and the warming effect of the Gulf Stream that flows past Scotland's west and north coasts. Orkney's natural sandstone geology results in alkaline waters which are relatively productive in biological terms (Berry, 1985). The lower catchment of the Eyrland burn is farmed intensively and it is likely that some enrichment of the aquatic environment occurs which could in turn stimulate trout growth, as observed in a similar situation elsewhere (Jonsson *et al*., 2011). This contrasts with areas like the north-west coast of Scotland,

Table 6.15: Sea trout smolt data sampled from other Scottish systems.

System, year	MFL (mm)	MSA (yrs)	Reference
Eyrland, 2004-2010	157.1 – 169.3	1.7-2.1	Present study
Tournaig, 1999-2001	167-190	-	Wester Ross Fisheries Trust, Tournaig smolt survey unpublished data.
North Esk, 1976- 1980	166-175	2.11-2.25	Pratten & Shearer (1983a)
Ewe, 1980 – 2001	~ 200	2.9-3.3	WRFT (2011)
Tweed, 1994 onwards	150mm	2.2	Tweed Foundation (2010)
Ayr, 2010	192	2.0	Ayrshire Rivers Trust (2010)
Graemeshall, 1931/32	170	2.3	Nall (1933)
St Mary's, 1931/32	167	2.3	Nall (1933)

where the Precambrian Lewisian and Torridonian geology result in mildly acidic and nutrient poor waters (SNH, 2001). Most Scottish studies also focus on larger rivers with catchments of greater altitude thereby resulting in colder growing conditions, especially when affected by snowmelt. It is perhaps not surprising therefore that a gradient in MSA is not apparent across Scotland.

Although larger smolts have been recorded at the extreme northern reaches of the sea trout's distribution (L'Abée-Lund *et al*., 1989), smolt size does not appear to vary with latitude (Jonsson & L'Abée-Lund, 1993) and the Eyrland data compared to other Scottish data do not undermine this theory. The minimum smolt size of 101mm was slightly smaller than observed in other populations while the maximum size of 233mm was not unusual. It has been suggested that smolt size varies directly with stream size, but only in very small streams of less than 0.25 cumecs average annual discharge (Jonsson *et al*., 2001). The discharge of the Eyrland burn is below this threshold, which may help to explain why smolts there were smaller than in other larger Scottish rivers such as the North Esk, Ayr and Ewe (Table). A consistent feature between years was the unimodal size distribution of smolts despite the presence of at least two or three age cohorts. This reflected a significant size overlap between age cohorts that prevented the determination of age by size alone.

The low MFL recorded in 2008 appeared to result from a lack of larger smolts. The length distribution of smolts in 2008 was the narrowest of the 7 years of sampling. While this may have been a natural result, it is perhaps noteworthy that a cormorant (*Phalacrocorax carbo*) was resident in the pool upstream of the trap for a period of days from late March to mid-April. Cormorants are known to predate salmonid smolts as they move downstream (Kennedy & Greer, 1988). The timing coincided with the start of the smolt run when the largest smolts are known to move downstream (discussed below) and may therefore explain why the overall MFL was lowest in 2008. The risk of predation may also have been increased if smolts were delayed upstream of the dam. The 2008 smolt catch of 333 was also the lowest of the four years the Wolf trap was operated, the next lowest being 420 in 2009.

The tendency for smolt size to decrease through the smolting period is in common with other studies (Pratten & Shearer 1983a; Euzenat *et al*., 1999; Bohlin *et al*., 1996). This decrease in size occurred in some years due to younger (smaller) smolts moving

downstream later in the spring. However, the trend was still apparent in 2008 & 2009 when over 90% of the smolt run comprised S2 smolts. This supports the findings of Bohlin *et al*. (1996) who postulated that the timing of downstream migration is size rather than age specific. In 2008, mean smolt size actually increased by the end of the run but there is little doubt this was caused by drought conditions, which delayed the downstream movement of smolts until late June, when in other years the run would normally be almost complete by the end of May. This drought extended across Scotland in 2008 and similar delays in smolt movement were noted elsewhere, *e.g.* Tournaig (Peter Cunningham, WRFT, *pers. comm*.). Although an increase in size might seem beneficial, it is likely that the net effect of such delays is negative, due to increasing water temperatures, decreasing dissolved oxygen and crowding in the pool upstream of the dam, factors which could encourage *inter alia* desmoltification as discussed previously. Fungal growth was also noted on many of the smolts when they finally did move downstream through the trap. Between drought and cormorant predation, 2008 appeared to be a bad year for migrating smolts in the Eyrland burn!

Freshwater growth

Growth curves showed that, in common with other studies, faster growth in freshwater led to migration at a younger age but smaller size (Jonsson *et al*., 2001). Jonsson & L'Abée-Lund (1993) reported that between populations, second year growth increments were directly related to smolt size, where increments of 4cm and 10cm equated to smolt sizes of 16cm and 20cm, respectively. Here in S2 smolts, which were the dominant age cohort in each year, the average second year increment over the sampling period was 77mm, which equated to a mean smolt size of 166mm at seawater entry (oMFL). Analysis of individual S2 data showed a strong relationship between both annual increments and smolt size. Individual data also showed that the size of S2 and S3 smolts at the end of winter was directly related to their size at seawater entry. This is perhaps not surprising except that the same relationship was not always present among S1 smolts. Spring growth characteristics in S1 smolts therefore appeared to be different from their older counterparts and it is suggested that this was due to contrasting rates of B-growth between smolt age cohorts.

In Chapter 5 it was clearly demonstrated that B-growth resulted in a significant size increase by the time of seawater entry, particularly in the youngest smolts. An indirect

relationship between size and B-growth was also suggested, *i.e.* small smolts achieved more B-growth than larger smolts, *irrespective of age*. Such a relationship in wild fish has not previously been reported in the literature. The analysis of individual fish data in this chapter provided strong evidence to support this hypothesis. For example, among S1 smolts, those which were smaller at the end of winter (so had exhibited slower growth prior to this point), subsequently grew faster and achieved more B-growth than S1 smolts which were larger at the end of winter. This could be described as "catch-up" growth, which brought S1 smolts to a more uniform size by the point of seawater entry. The same relationship was noted in S2 smolts. Overall this shows a subtle growth dynamic during the freshwater growth period. It is perhaps too simplistic to divide pre-smolts into slow and fast growing fish. It was evident here that within the same age cohort, individual fish showed periods of slower and faster growth relative to their counterparts, prior to seawater entry. This behaviour could also be described as a type of compensatory growth, *i.e.* the ability to catch up in size/weight through accelerated growth after a period of slow growth, which has been described in various studies. Nicieza & Metcalfe, (1997) found that juvenile Atlantic salmon which were reared at reduced temperatures or on reduced rations entered a compensatory growth phase after return to normal conditions, although only the group which were subject to reduced rations were able to gain a similar size to the control group after return to of full rations. In another hatchery experiment that involved Rainbow trout (*Onchorynchus mykiss*), Jobling & Koskela (1996) observed the greatest level of compensatory growth in the individuals that showed the poorest growth during food restriction. This contrasted with the findings of Johnsson & Bohlin (2006) who, in a combined laboratory/wild experiment on brown trout, found that compensatory growth was not proportional to the amount of growth restriction. Increased levels of mortality were also associated with growth restriction. The study by Nicieza & Metcalfe, (1997) was interesting in that it found the strongest compensatory response in pre-migratory rather than non-migratory individuals. The results of this study reflected the findings of Jobling & Koskela (1996), *i.e.* catch-up growth was proportional to the extent of growth restriction, although whether this is a valid comparison is open to debate. It could be argued that growth restriction in this study was evident in individuals that were smaller at the end of the winter period prior to entering the B- (compensatory) growth phase. Smaller pre-smolts may have originated from the upper areas of the catchment, as it was demonstrated in Chapter 4 that that growth rate decreased with upstream distance. The

growth "restriction" in this case might result from a combination of factors such as decreased temperature, food availability or habitat.

While initial size appeared to be the primary determinant of B-growth within sample years, a secondary effect was also observed between sample years, and was related to spring temperatures. Across the sampling period a direct relationship between spring grwing conditions and B-growth was seen in S1, S2 and S3 smolts. A similar relationship was reported by Fahy (1990) in S2 smolts. In 2010, when spring growing conditions were poorest (coldest) in the sample period, B-growth was significantly lower in all three of the age cohorts than it was in 2007 (the only other year when all three age cohorts were well represented) when conditions were much warmer. An additional point of interest between these two years was that in the cold conditions of 2010, the amount of B-growth exhibited by S1 smolts increased with time through the sampling period, which might be expected. However in the warmer spring of 2007, no relationship existed between B-growth and date of capture. It is possible that B-growth was limited in 2010 by the colder water temperatures and increased in line with increasing temperatures. In the warmer spring of 2007, temperature was perhaps not limiting and therefore B-growth was not affected by sampling date.

Target smolt size in anadromous Salmo trutta

B-growth data provided a strong indication of an urge in smolting fish to maximise their size before seawater entry. Furthermore, the data suggested the "recognition" of a threshold or target size which was particularly strong in the smallest smolts as they exhibited the largest size increase prior to seawater entry. Before rejecting the notion of a threshold size, Økland *et al*. (1993) noted that migration in smolts of both Atlantic salmon and sea trout occurred in the spring after reaching a mean size of 10cm by the previous winter, similar to that found here for S1 trout smolts at the end of winter. Alm (1950) reported size of >13cm in smolting brown trout. Nicieza & Braña (1993) suggested that Atlantic salmon smolts in a Spanish population had to reach 100mm by their first winter and were a minimum of 130mm at smolting. What is not made clear in these studies is the moment at which these sizes are measured - size at end of winter, at seawater entry or somewhere in between. This is an issue in the existing literature that makes it difficult to accurately compare smolt sizes between populations. Directly comparable data were of course collected from three other Orkney populations and detailed in the previous chapter. The same trends were noted between S1 and older

smolts and the mean size of S1 smolts at seawater entry varied from approximately 130-135mm. These data along with the aforementioned results, suggest that a threshold size for seawater entry, if it exists, may vary within a relatively narrow size range. Furthermore, the very strong role of B-growth in determining smolt size at seawater entry is clear.

However, the analysis of individual smolt data in this chapter showed a more complex situation than suggested from the mean size data for each age cohort. Individual data showed that 95% of S1 smolts were ≥130mm at the moment of sampling, which was judged very close to the point of seawater entry. Over 99% of S2 smolts were ≥130mm at sampling while less than 1% exceeded 130mm at age one. In S3 smolts, none exceeded 130mm at age one, but 24 (31.6%) exceeded 130mm at age two, reflecting the findings of Økland *et al*. (1993), whose observation was based on the mean size of the different age cohorts. This forces the same conclusion, that factors other than absolute size must be involved in the mechanism that controls the passage of smolts to the sea. It is perhaps worth noting however that overall, S3 smolts were the least common of the three smolt ages found in the Eyrland burn and only 24 individuals exceeded the 130mm target size at age two. Furthermore, their number included individuals which should have smolted at age two (they were sampled in smolting condition) but did not until the following year. The occurrences of these repeat smolts and the possible reasons for this behaviour were discussed earlier. If repeat smolts are discounted then the percentage of S3 smolts that exceeded the 130mm target size dropped to 24% (comprising 18 individual fish over the four year sampling period). The role of S3 smolts therefore appears the central issue of the threshold size discussion. It was stated earlier that the number of repeat smolts found was a minimum estimate and therefore, until more information is available on the proportion of S3s that are repeat smolts, and given the relatively small numbers involved, it is perhaps unreasonable to completely reject the notion of a threshold size in this population.

In conclusion, this chapter has revealed several notable aspects of brown trout migration. The possible role of the new moon as a stimulus to downstream movement during stable or falling water levels and the ability of brown trout smolts to de-smolt in one year and re-smolt the following year have not previously been reported for this species. Strong evidence was found of an inverse relationship between size at end of winter and the amount of B-growth achieved by the time of seawater entry, which was

present between and within age cohorts. B-growth therefore resulted in a significant increase in smolt size in the period immediately before seawater entry. Finally, it was shown that majority of smolts produced by the Eyrland population were equal to or greater than 130mm in size (FL) at seawater entry which is suggested as a target size for smolting in this population. This hypothesis was undermined by a small number of S3 smolts, which were apparently large enough to smolt at age two but did not. This number included fish that were in smolting condition at age two but delayed their passage to sea until smolting again at age three. Until further information on the occurrence of these fish among S3 smolts is available then the two-stage threshold model cannot be discounted for this population.

CHAPTER 7. UPSTREAM MIGRATION OF SEA TROUT IN THE EYRLAND BURN, ORKNEY, 2007 & 2009

7.1 Introduction

Sea trout smolts are voracious feeders and enter a phase of rapid growth after they enter the sea as they benefit from a rich marine diet (Jonsson & Jonsson, 1998). Growth rate during the first summer tends to be greatest and decreases in subsequent years, particularly with the onset of maturity (Jonsson, 1985). Marine growth rates vary within and between populations. It has been reported in both Atlantic salmon and sea trout that smaller smolts grow faster at sea than larger smolts (Jonsson & L'Abée-Lund, 1993; Nicieza & Braña, 1993). Pratten & Shearer (1983b) found that younger (smaller) smolts grew faster than older smolts at sea, and by the time of their return to freshwater (as finnock), there was no difference in size between age groups. However, it has also been reported that no relationship exists between smolt size and post-smolt growth at sea (Friedland *et al*, 2006). In a review of data for 102 European sea trout populations, mean first year growth at sea was found to vary from 80mm - 220mm (Jonsson & L'Abée-Lund, 1993).

Between populations, there is a general decrease in growth rate with increasing latitude due to decreasing sea temperatures. However, longevity increases with latitude so that in northern areas, *e.g.* north Norway, sea trout are characterised by slower growing, older fish, which typically reach 10 years of age. In contrast, southern populations, *e.g.* in Spain and France, comprise faster growing fish which generally do not grow older than five years of age (L'Abée-Lund *et al*., 1989; Jonsson, B. *et al.*, 1991; Jonsson & L'Abée-Lund, 1993)[1]. Size however does not appear to follow a latitudinal trend. Mean size at maturity has been reported to vary from 19.9cm – 75.8cm (Jonsson, 1981, L'Abée-Lund *et al*., 1989; L'Abée-Lund, 1991; Jonsson *et al*., 2001). Adult size has been linked to conditions in the home stream. Jonsson *et al*. (2001) reported a direct relationship between mean size at maturity and stream size. Bohlin *et al*. (2001) also reported that as freshwater migratory costs increased, *i.e.* distance and altitude to spawning grounds, adult size increased. Both studies underpin the theory that sea trout size is directly related to size of the home stream and exemplify adaptations to the local

[1] Incidentally, mean age at maturity in populations at a similar latitude to Orkney (59°) varied from 5/6 yrs for males and 6/8 yrs for females (Jonsson & L'Abee-Lund, 1993).

environment. It is also possible therefore that stream size could influence mean age at maturity, causing deviations from the general relationship with latitude described above. Growth rates also vary between male and female fish. Females are generally more numerous, take longer to reach maturity, live longer and therefore are larger than males (Berg & Jonsson 1990; Jonsson, B. *et al.*, 1991).

Genetic evidence suggests that sea trout exhibit a high degree of fidelity to their natal stream with rates of straying to non-natal streams of between 1-3% (Ferguson, 2006). Higher rates of straying may occur between small, closely neighbouring populations, as suggested from work on the Baltic island of Gotland (Laikre *et al.*, 2002). It should also be noted that sea trout might stray into other systems without actually spawning there (Pratten & Shearer, 1983b). The seasonal timing of freshwater return is closely related to the size of the home stream or river. In larger systems, sea trout return earlier in the year and spend much longer in the river prior to spawning than is the case in smaller streams. Catch data from the River Ewe in Scotland, collected prior to the collapse of the fishery, show that the bulk of fish were caught in July (Butler & Walker, 2006). In more southern rivers, *e.g.* the River Bresle, France, the return migration may occur earlier, in May (Euzenat *et al.*, 2006). However, in smaller streams, the return occurs in October and November (Nall, 1933; Titus & Mosegaard, 1992). Late arrival to small streams may be an adaptation to the increased risks associated with returning to small systems, where suitable habitat for relatively large fish is restricted, particularly during low water flows. On the other hand, it just may be physically impossible for returning sea trout to access small systems without sufficient water flow (Titus & Mosegaard, 1992). The factors which control the exact timing of upstream movement might also vary with stream size. As suggested above, in small streams, elevated water levels might be required to gain entry to freshwater from the sea. Elevated levels might also be required to negotiate obstacles such as waterfalls, dams and fish passes although in such cases, very high water flows might also inhibit progress and upstream passage might only occur at an intermediate water level (Jonsson & Jonsson, 2002; Svendsen *et al.*, 2004).

Spawning populations range widely in size. In small rivers, spawning might be severely reduced in drought years (Titus & Mosegaard, 1992). When spawning does occur, female sea trout may be attended by both anadromous and resident male fish. The proportion of males among returning anadromous fish varies from 27% to 49%

(Campbell, 1977; Jonsson *et al.,* 2001) and so in many cases males are likely to spawn with more than one female. Resident males also participate in spawning through "sneak" fertilization (Campbell, 1977; Dellefors & Faremo, 1988). The fecundity of female fish varies directly with size but also between fish from different populations, for which there may be both genetic and/or environmental reasons. Estimates of egg production for 500g females range between 909 and 1537 (Jonsson & Jonsson 1999, Maisse & Bagliniere 1991). Egg losses (*i.e.* the difference between egg production and eggs per redd), may result from egg retention within the female or eggs lost downstream during spawning, and increase with fish size. It was estimated that while a fish of 240mm might successfully deposit 100% of its eggs within the redd, a female of 650mm might only succeed in depositing 79%.

This chapter examines the return migration of sea trout to the Burn of Eyrland, a small coastal stream in the Orkney Islands. The specific aims of this survey were:

- to examine the size, age and gender characteristics of returning sea trout;
- to examine the timing of the return to freshwater and the factors which influence upstream movements; and
- to investigate patterns of marine growth and survival, making use of existing smolt data where necessary.

The results of these investigations are provided below, which represent the final instalment of the work conducted during this thesis.

7.2 Methods

The reader is referred to Chapter 2 for a detailed description of methods used in this phase of work. Summaries are provided below.

7.2.1 Upstream sampling

Sea trout returning to the Eyrland burn were sampled in autumn 2007 and 2009. THis was achieved using an upstream trap installed on the upstream exit of the fish ladder, located approximately 100m above the tidal limit of the burn. The trap was checked once daily or more often during periods of peak migration activity and/or high water flows. A full description of the trap construction is provided in Chapter 2.

7.2.2 Fish processing

All fish were processed according to the methods for fish processing found in Chapter 2. After processing they were allowed to recover and released in the pool upstream of the trap.

7.2.3 Scale reading

Scale reading was carried out according to the method described in Chapter 2. It should be noted that the estimation of smolt size by back-calculation using scales from older sea trout was done using the end of the last winter annulus in freshwater as the moment of seawater entry. The validity of this method is discussed in section 7.4 (Discussion) where the opportunity is taken to adjust the estimates using B-growth data from the previous chapter.

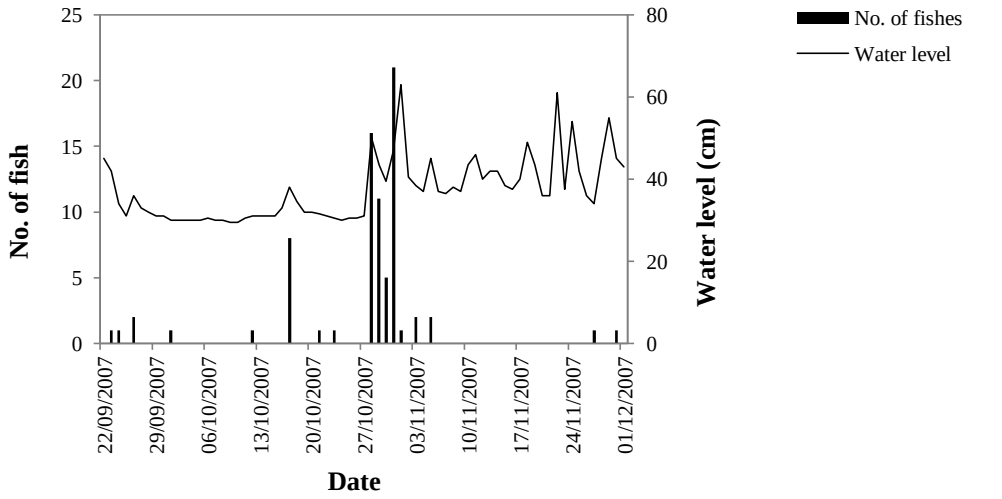
7.3 Results

7.3.1 Catch summary

Over the two year sampling period, 194 sea trout were caught moving upstream on the Burn of Eyrland. In 2007 a total of 72 sea trout were caught in the trap. The first sea trout was caught on the 23rd September with the last recorded on the 30th November. The majority (74%) were caught over a 4 day period from the 28th – 31st October. In 2009, a total of 122 sea trout were caught between the 24th September and the 30th October. Passage through the trap was more spread out and occurred in three distinct pulses on the 4th-7th, 14th-15th and 23rd-25th October. The daily catch in each year is shown in Figure 7.1 along with daily water level. Daily mean water temperature recorded at the trap site through the survey period in each year is shown in Figure 7.2. Raw water temperature data are provided in Appendix L. No mortalities were observed among the sea trout caught in the trap and they were all released into the pool upstream after processing. Raw data for each sample year is provided in Appendix S.

In 2007, 30 (41.7%) out of the 72 sea trout trapped were marked (clipped or VIE tagged) indicating they had been trapped previously as smolts leaving the burn (see Chapter 5). In 2009, 43 (35.2%) out of 122 sea trout were marked. VIE tagged smolts from 2007 were also been caught at sea by local anglers. Seven recaptures were reported in late 2007 (finnock) and early 2008 (1SW), all in the Scapa Flow area. Recapture locations are shown in Figure 7.3 and ranged from the Eyrland burn mouth to the Bay of Houton, approximately 7km away.

2007



2009

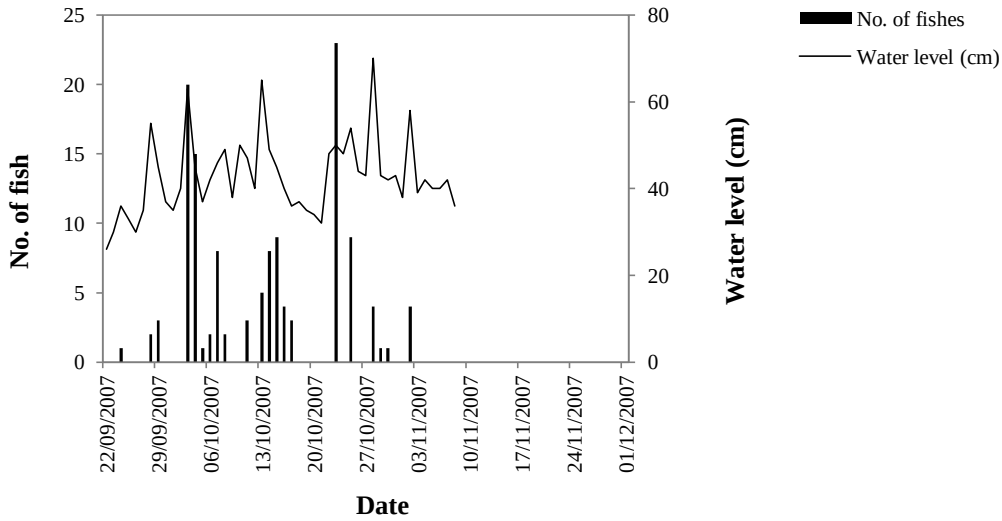


Figure 7.1: Daily records from Eyrland upstream trap operated in 2007 and 2009, showing date, fish trapped and water level.

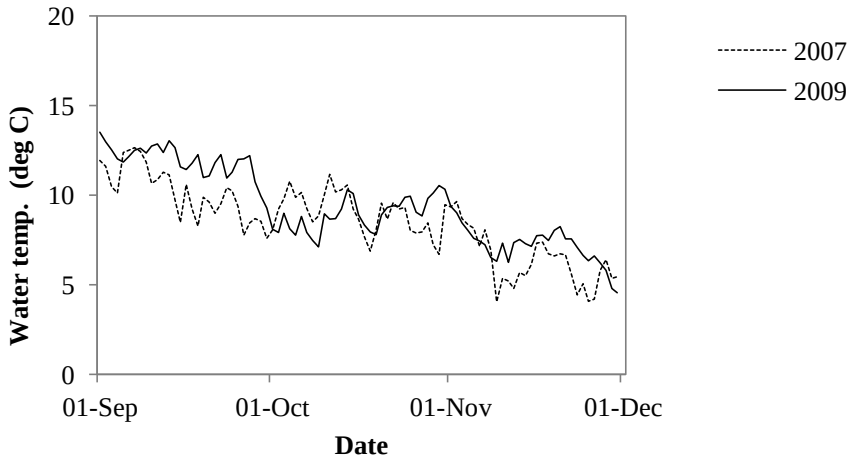


Figure 7.2: Daily mean water temperature recorded at the Eyrland fish trap from 1st September to 1st December 2007 & 2009.

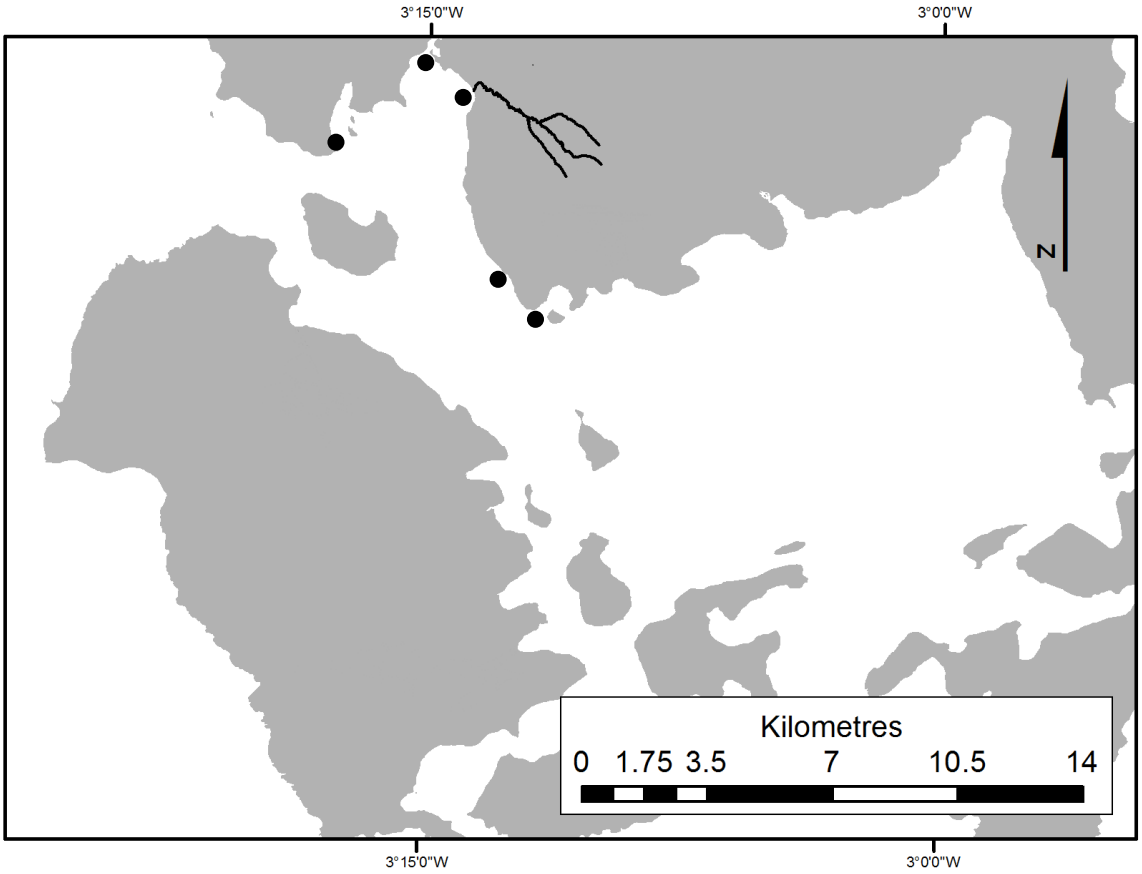


Figure 7.3: Recapture sites for Eyrland post-smolts in the local sea trout fishery (N=7).

7.3.2 Run timing & controls

The occurrence of significant catches of sea trout (defined as a catch of >5% of the total) is shown in Table 7.1 along with water level and lunar phase. Out of the 12 significant runs which occurred in the two sample years, ten were associated with increases in water level which occurred less than 48hrs before the run occurred. GLM (stepwise) analysis showed that change in water level was a significant positive influence ($F(1,10) = 9.25$, $p = 0.012$) on the daily catch in the trap and the relationship did not differ between years (Table 7.2). Change in water level explained 42.9% of the variation in daily catch. Daily catch was not related to absolute water level or timing with respect to lunar phase.

Sea trout moved upstream both at night and during the day. At peak periods of migration and water flow, the trap was inspected twice daily. In 2007, 13 (18.1%) out of the total catch of 72 sea trout were removed from the trap on the second daily

Table 7.1:The occurrence of significant upstream movements in relation to water level and moon phase, Eyrland burn, 2007 & 2008.

Year	Date	No. trout	% Total Run	Water level (cm)	ΔWater level, 48hrs (cm)	Days (+/-) to new moon
2007	17/10/07	8	11.1	38	7	+6
	28/10/07	16	22.2	50	19.5	-12
	29/10/07	11	15.3	43.5	19	-11
	30/10/07	5	6.9	39.5	-10.5	-10
	31/10/07	21	29.2	47	7.5	-9
2009	3/10/09	20	16.4	63	18	-15
	4/10/09	15	12.3	45	23	-14
	7/10/09	8	6.6	46	9	-11
	14/10/09	8	6.6	49	10	-4
	15/10/09	9	7.4	43	-7	-3
	23/10/09	22	18.0	50	18	+5
	25/10/09	9	7.4	54	6	+7

Table 7.2: GLM analysis of the relationship between environmental variables and daily catch in the Eyrland trap in 2007 and 2009.

Source	DF	Adj SS	Adj MS	F-Value	P-Value
- Change in water level	1	1.192	1.1920	9.25	0.012
Error	10	1.288	0.1288		
Total	11	2.480			

inspection which occurred by 1800hrs (the trap was emptied the same morning). In 2009, the equivalent figure was 34 (27.9%) out of 122. Additional sea trout may have moved upstream in daylight hours on other days but were not included in these estimates as the trap was not checked before darkness.

Water temperature at the start of the migration in each year was similar. Average daily water temperature on the 24th September was 10.3°C and 11.3°C in 2007 and 2009, respectively. In 2007 the end of the run occurred on the 30th November by which time the daily average water temperature had dropped to 5.5°C. In 2009, the upstream migration finished earlier on the 30th October, when the average water temperature was 10.5°C. Average water temperatures in October, during which the vast majority of sea trout moved upstream in both sample years, were similar (9.1°C in 2007 and 9.9°C in 2009).

7.3.3 Population structure

The samples from 2007 & 2009 were pooled for the analysis of population structure. The total sample of 194 sea trout comprised four different sea age cohorts: 0+ (finnock), 1+, 2+ and 3+. Female trout represented 68.6% of the sample, males 25.8% with the gender of the remaining 5.6% undetermined. Composition of the sample in terms of sex and age is detailed in Table 7.3. In terms of sea age, the majority of females were aged 1+ (59.4%) although fish aged 2+ were also common (31.6%). Female finnock and fish aged 3+ each represented <5% of the sample. Among males, finnock (50.0%) and fish aged 1+ (44%) predominated with a small number aged 2+ (6%). In the entire sample, the ratio of female to male sea trout was 2.7:1 and among fish aged 1+ or older (N = 156), females outnumbered males by a ratio of 5.1:1. A length frequency analysis for pooled data is shown in Figure 7.4. This illustrates the numerical dominance of females and their tendency to grow larger than male fish. However, size cohorts for each age group were indistinct, particularly for females, indicating an overlap in the size range for each age cohort.

Table 7.3: Composition of returning sea trout in the Eyrland burn by sex and sea age, 2007 & 2009. Numbers in each group were extrapolated from sub-sample of 133 fish for which sea age was determined from scale samples.

	Total in sample		
Sea age (yrs)	**Female**	**Male**	**unknown**
0+	6	25	7
1+	79	22	2
2+	42	3	-
3+	6	0	-

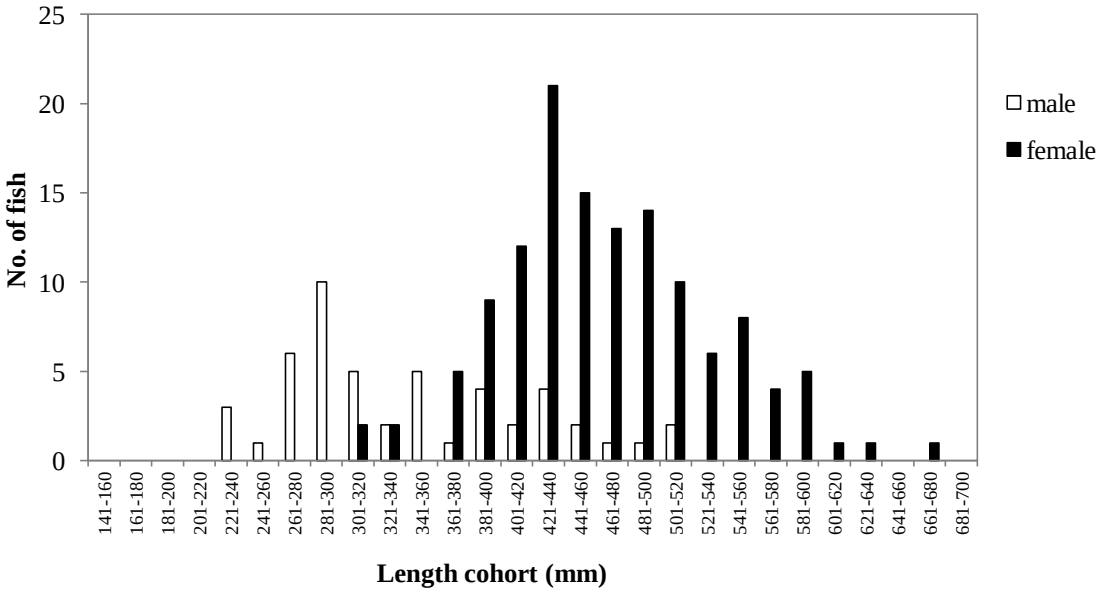


Figure 7.4: Length frequency analysis (by sex) for sea trout caught in the Eyrland trap, using pooled data from 2007 & 2009.

7.3.4 Smolt age and size

The proportion of different smolt ages in returning sea trout as well as their mean size at smolting is shown in Table 7.4. The majority of returning sea trout were S2 smolts, which represented 77% of the pooled dataset. The remainder of the sample comprised fish which had smolted at S1 (16%) and S3 (7%) and the MSA was 1.9 years. Sea trout which smolted as S2s were the longest lived amongst the sample, reaching a maximum sea age of 3+. Sea trout which smolted as S1s reached a maximum sea age of 2+ while those which smolted S3s only achieved a sea age of 1+. Mean size at smolting, for each age cohort varied from 114.1mm for S1s to 186.5mm for S3s. Note that these estimates were made by back calculation and assumed that seawater entry occurred at the end of the last winter annulus in freshwater. These estimates and the relevance of B-growth in the estimation of smolt size are addressed later.

Table 7.4: Back-calculated size at smolting (at end of winter annulus prior to migration) for sea trout returning to the Eyrland burn, 2007 & 2000.

Smolt age (yrs)	Proportion of sample	MFL at smolting (mm)
S1s	16%	114.4
S2s	77%	167.7
S3s	7%	186.5

7.3.5 Marine growth

The largest female trout captured was 664mm and had a sea age of 3+ years. The largest male was 520mm with a sea age of 1+ years. Average marine growth at time of capture for different aged males and females is detailed in Table 7.5 and illustrated in Figure 7.5. This shows that in general, females were larger than same-aged males. This difference was significant in trout with a sea age of 0+ (finnock) and 1+ years. There were too few males aged 2+ sea winters to make a valid comparison and there were no males aged 3+ sea winters.

Figure 7.6 shows back-calculated growth curves by smolt age and sea age (excluding finnock which were defined as trout returning to freshwater in the first winter after smolting). This illustrates a similar marine growth trajectory in trout which smolted as S2 and S3 smolts, with S1 smolts exhibiting slightly less growth in each year. Analysis by one-way ANOVA showed that size at age differed significantly between groups which smolted at different ages. At smolting, trout which smolted as S2 and S3 smolts were similar in size and both were significantly larger than those which smolted as S1 smolts ($F(2, 112) = 27.87$, $p < 0.001$). After one year at sea there was a significant difference in mean size between returning sea trout of different smolt ages ($F(2, 86) = 6.49$, $p = 0.002$). Post hoc testing showed that trout which smolted as S2s were significantly larger than those which smolted as S1s. However, trout which smolted as S3s did not differ significantly in mean length from the other two groups. Only three trout were aged 3.1 years and as the standard deviation of length was relatively high. After two years at sea (only represented by trout which smolted as S1 and S2 smolts), there was no significant difference in mean size between the different smolt ages ($F(1, 25) = 0.79$, $p = 0.383$).

Table 7.5: Mean size of different aged male and female sea trout sampled from the Burn of Eyrland in 2007 & 2009.

Sea age (yrs)	MFL± all fish (mm)	Female		Male		ANOVA result (largest)
		N	MFL (mm)	N	MFL e (mm)	
0+	284.7	6	333.8	25	279.0	Females, $F(1,19) = 18.65$, $p < 0.001$
1+	425.3	79	433.3	22	407.6	Females, $F(1,67) = 4.59$, $p = 0.036$
2+	516.1	42	518.1	3	487.0	Similar, $F(1,29) = 1.28$, $p = 0.267$
3+	573.0	6	559.8	0	-	No comparison (females only)

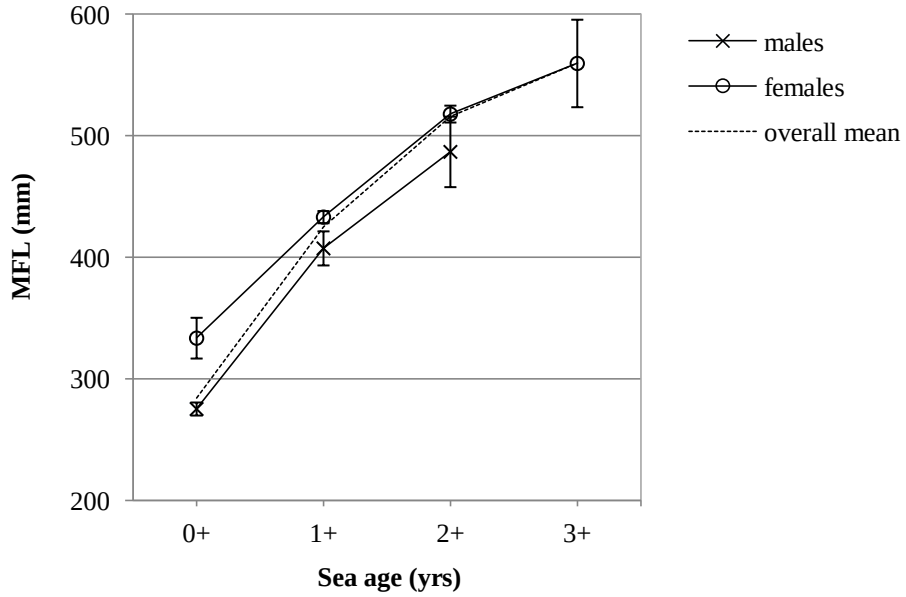


Figure 7.5: Mean size (MFL ± se) of different aged male and female sea trout sampled from the Burn of Eyrland in 2007 & 2009. The overall mean (all trout) is shown for comparison (dotted line).

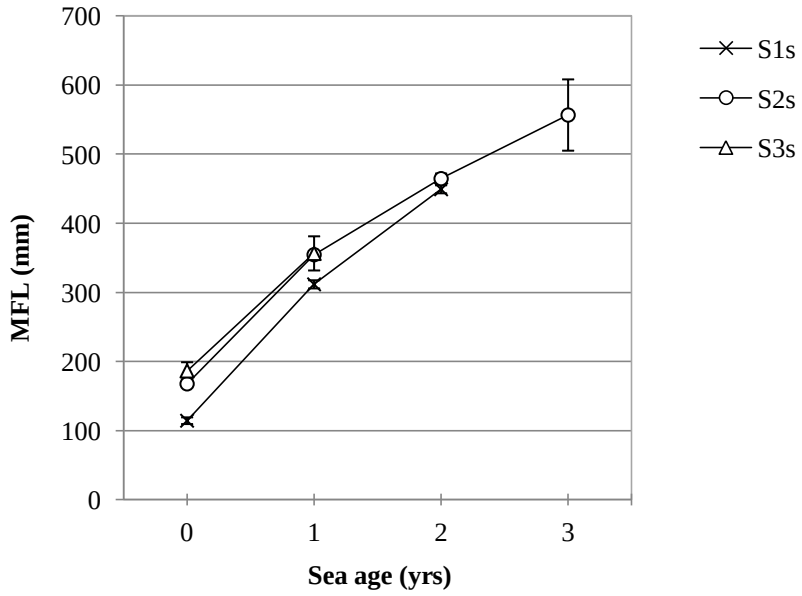


Figure 7.6: Marine growth curves (freshwater and marine phases) estimated by back calculation for sea trout of different smolt ages returning to the Eyrland burn, 2007 & 2009 (excluding finnock). Sizes presented as MFL ± se at each age.

Table 7.6: Annual marine growth increments estimated by back calculation for sea trout of different smolt ages returning to the Eyrland burn, 2007 & 2009 (excluding finnock).

Smolt age (yrs)	Annual marine growth increments (mm)		
	1st year	2nd year	3rd year
1	196.2	140.1	-
2	184.7	85.2	80.3
3	160.4	-	-

Table 7.6 details the average annual marine growth increments in fish of different smolt age. First year growth declined with smolt age. S1 smolts achieved an annual increment of 196.2mm, while S2 and S3 smolts achieved increments of 184.7mm and160.4mm, respectively. However, their smaller initial size meant that after one year at sea, fish which had smolted as S1s were still smaller than those which had smolted as S2s or S3s. In their second year at sea, S1 smolts achieved a mean increment of 140.1mm, while growth in S2 smolts dropped to 85.2mm. This allowed S1 smolts to catch up with S2 smolts and exceed them in average size after two years at sea. S3 smolts living two years at sea were not present in the sample. In their third year at sea, S2 smolts showed an average growth increment of 80.3mm. No other smolt cohort of this sea age was present in the sample to make a comparison.

7.3.6 Return rates

Return rates were estimated for different age cohorts of trout in both the sample years and are detailed in Table 7.7. Return rates were only estimated when there was good data available for the corresponding smolt year, *i.e.* in years when the Wolf trap was operational (2007 – 2010). Therefore, in 2007, only return rates for 0+ SW trout (finnock) could be estimated, while in 2009 it was possible to estimate return rates for trout aged 0+, 1+ and 2+ SWs based on smolt runs in 2009, 2008 and 2007, respectively. Furthermore, return rates were based on the assumption that all trout caught in the trap had originally smolted from there. Unfortunately, as the upstream trap was only operated in two years, it was not possible to follow a single cohort of smolts completely through their marine phase, which apparently would have required four consecutive year's operation in order to capture fish returning at sea ages of 0+, 1+, 2+ and 3+.

Table 7.7: Estimated return rates for different age cohorts of sea trout returning to the Eyrland burn, 2007 & 2009. The total number of trout caught in 2009 (112) excludes fish aged 3+ sea winters as a reliable estimate of smolt output was not available for 2006.

Year	Sea age (yrs)	Smolts caught in year of migration	Total caught	Return rate %
2007	0+	519	16	3.1
2009	0+	624	27	4.3
	1+	333	64	19.2
	2+	519	21	4.0
	Total 0+, 1+, 2+	1476	112	7.6

Return rates for finnock were approximately 3-4% in both years. The return rate for 2+ trout trapped in 2009 (finnock in 2007) was similar at 4%. The return rate for 1+ fish trapped in 2009 (smolt year 2008) was the highest for any individual age cohort at 19.2%, reflecting that fact that this age cohort was the most numerous in the 2009 sample. The overall return rate for sea trout returning to the burn in 2009 was 7.6% although this estimate would not account for fish which had made more than one return visit to freshwater, *e.g.* repeat spawners. In this case the estimate may represent an over-estimate of the actual return rate, which might alternatively be described as the "apparent" survival rate.

7.4 Discussion

In each of the two sample years, most sea trout moved from the sea into the Burn of Eyrland in October. Upstream movements were associated with increases in water level, and while most fish moved upstream in darkness a significant proportion also moved upstream in daylight. Among the returning sea trout, females were more numerous, larger and older on average than males. Among fished with a sea age of 1+ or older, females outnumbered males by approximately 5:1. Most fish had smolted as S2s. Marine growth rates were greatest in the first year at sea and appeared to exhibit an indirect relationship to age of smolting. Fish which smolted as S1s maintained a comparable growth rate in their second year at sea while growth in S2 fish was considerably reduced. In 2009, based on the number of smolts leaving the burns in 2008, the survival rate of 1+ (sea age) fish was approximately 20%.

Catch & run timing

The numbers of sea trout caught returning to the Eyrland burn suggested a relatively healthy population in comparison to some other small Scottish systems. In the Tournaig burn for example, between 1999 and 2012, no more than 20 sea trout returned in any year (Wester Ross Fisheries Trust, 2013). In the Shieldaig system, returns of wild fish between 1999 and 2007 did not exceed 30 fish (Marine Scotland Science, 2010). The capture of sea trout marked previously as smolts leaving the burn indicate fidelity to the home system. However, in each sample year, less than half the catch was marked. A higher proportion of marked fish was expected in 2009, as many more smolts had been marked in the preceding years than in 2007. There are two possible explanations for the high proportion of unmarked fish in each year's samples. Firstly, if smolt trap efficiency was poor then a large number of smolts would evade capture and get to sea unmarked. The second possibility is that the unmarked fish originated from different populations. The calculation of smolt trap efficiency was hampered by the occurrence of de-smolting, as described in Chapter 6, but minimum rates varied between years from 40 to 70%. It is not unreasonable to conclude that at least some of the unmarked fish returning to Eyrland had originated there. Straying rates of around 1-3% which have been reported elsewhere (Ferguson, 2006) would not account for the large number of unmarked fish, but straying rates are likely to vary from region to region and higher rates are suggested to apply in areas like Orkney with small, closely neighbouring populations (Laikre *et al.*, 2002). The nearest sea trout system to Eyrland are the linked

lochs of Harray and Stenness (with a catchment of approximately 120km^2) which enters the sea approximately 1 mile away from the Eyrland burn. It is likely to produce a large number of smolts that may pass the mouth of the Eyrland burn. Finnock are known to enter other river systems although they do not necessarily spawn there (Pratten & Shearer, 1983b). This study has also shown that in Orkney, finnock may even enter burns which contain no other trout (see Chapter 3).

In both sample years, the majority of sea trout were caught in October which reflects other observations that sea trout from small systems return later in the year than those from larger systems (Titus & Mosegaard, 1989; Butler & Walker, 2006; Euzenat *et al*., 2006). A similar result was obtained by Nall (1933) in his study of the Graemeshall and St Mary's sea trout populations in Orkney in the early 1930s. Within the short period of the migration, change in water level was a significant influence over upstream movements, with the vast majority of fish moving upstream shortly after increases in water level, as observed elsewhere (Campbell, 1977; Svendsen *et al*., 2004). However, the strength of this association may have been partly due to the location of the trap, at the top of a fish ladder, which was passable only in medium to high flows. Indeed, upstream movements of sea trout may also occur in stable or falling water levels (Jonsson & Jonsson, 2002). It is likely for any particular stream or river the water level required for upstream passage will vary depending on local conditions and the presence of obstacles. Although the majority of sea trout were trapped during darkness, a significant proportion moved upstream during daylight hours. These instances generally occurred after spate conditions.

Population structure

Among the sea trout returning to the Eyrland burn, females were more frequent, larger and longer living on average than male trout, as found in other studies (Alm, 1950; Campbell, 1977; Jonsson, 1982; Euzenat *et al*., 1999). The age distribution among returning sea trout, with fish of one and two sea winters being most common and no fish older than three sea winters, suggests a relatively fast growing population. Using the method of Jonsson & L'Abée-Lund (1993), the mean sea age at maturity of the Eyrland population would be 1+, or approximately 1.5 years, which is typical of other populations at the same latitude found by those authors. The same sea age at maturity was found in fast growing French populations (Euzenat *et al*., 1999).

Table 7.8: Size at smolting in sea trout returning to the Eyrland burn in 2007 & 2009, estimated by back calculation. Estimates adjusted by the addition of mean B-growth exhibited by each smolt age. Mean smolt size from downstream trap surveys included for comparison. B-growth and smolt size data detailed previously in Chapter 6.

Smolt age in returning sea trout (yrs)	Returning sea trout			Observed smolt size 2004 – 2010 (mm)
	Back calculated MFL at smolting (mm)	Mean B-growth 2004 – 2010 (mm)	Adjusted MFL at smolting (mm)	
1	114.4	37.5	151.9	144.5
2	167.7	17.6	185.3	165.5
3	186.5	9.1	195.6	181.5

Smolt age among returning fish reflected the age structure in emigrating smolts sampled between 2004 and 2010, *i.e.* S2 were dominant, followed by S1s then S3s, and the MSA in returning fish (1.9yrs) matched the MSA in emigrating smolts detailed in Chapter 6. Size at smolting for returning fish can be compared to empirically collected smolt data recorded between 2004 and 2010 at the downstream trap (Table 7.8). This shows that while there is relatively good agreement between the two estimates for S2 and S3 smolts, the size of at smolting for S1 fish is considerably lower (by 26.3%) than the empirical data. The reason for this is most likely because smolt size in returning fish was estimated by back calculation and the moment of smolting was taken at the end of winter prior to migration. It was demonstrated in Chapters 5 & 6 that B-growth, which occurs in freshwater after the winter annulus, can cause a significant size increase by the time of seawater entry and that B-growth was greatest in the youngest smolts, *i.e.* S1s. Table 7.7 also shows mean B-growth for each smolt age cohort estimated from smolt sampling between 2004 and 2010. After adding B-growth, the adjusted size for S1 smolts is much closer to but just exceeds the empirical data. The adjusted estimates for S2 and S3 smolts also exceed the empirical data. It is unclear why all three estimates should exceed the empirical data. The data suggest that in each age cohort, the fish that survived at sea long enough to return as mature sea trout were those which were larger than average at smolting. This data therefore support the presence of a positive relationship between size at smolting and survival rate at sea (Hoar, 1976).

The above discussion highlights a major disadvantage in the estimation of smolt size using scale samples from older fish which have undergone a marine growth phase. Scale reading techniques typically use the moment at the end of last winter annulus as the moment of sea entry and the start of marine growth. As the previous chapter

demonstrated, smolts may not enter the sea for some weeks after the end of the winter annulus, during which B-growth can significantly increase their size before they actually enter the sea and begin the marine growth phase. Failing to account for B-growth risks underestimating smolt size at the point of seawater entry, the moment which in the author's view, is more meaningful from an ecological viewpoint. It is somewhat surprising that this potential source of error is not discussed in any study using this method (L'Abée-Lund *et al.*, 1989; Jonsson & L'Abée-Lund, 1993; Jonsson, B. *et al.*, 1991; Jonsson *et al.*, 2001). Moreover, studies like that of Økland *et al. (*1993), which rejected the hypothesis of a size threshold for smolting in sea trout, should be considered in this light. However, it is difficult to suggest a solution to this issue, as B-growth tends to be difficult to distinguish on scale samples. In the meantime, it seems clear that direct observation of smolts is required to accurately assess smolt size at seawater entry.

Marine growth

A comparison of marine growth rates in the Eyrland populations with other Scottish populations is illustrated in Figure 7.7. As ever, some caution is required in such cases, particularly when the studies are spread over several decades. The only similar data for Orkney relate to the Graemeshall and St Mary's systems studied by Nall (1933). At the time, sea trout from those systems were found to exhibit very rapid marine growth and in Scotland were second only to sea trout from the Tweed. The present study suggests that growth among sea trout from the Eyrland burn is slower although contemporary data from Graemeshall and St Mary's would allow a more valid comparison. However, the Eyrland data fall within the range exhibited in other Scottish systems studied more recently (Walker, 1987; Solomon, 1995). The comparison of annual growth increments (size at 1, 2, 3 sea winters) also show that the Eyrland data fit within the range of published marine growth rates. L'Abée-Lund *et al.* (1989) studied 34 populations in Norway between 58° and 70° north and found that first summer growth varied between 79mm and 204mm although populations on a similar latitude to the Orkney Islands (59° N) grew between 160mm and 204mm on average. Jonsson & L'Abée-Lund (1993) examined 102 populations across Europe and found first year marine growth varied between 80mm and 220mm. Populations located between 58° and 60° N had a range of 90mm to 200mm. Nall (1933) estimated first year marine growth of approximately 190mm and 170mm in the Graemeshall and St Mary's populations, respectively.

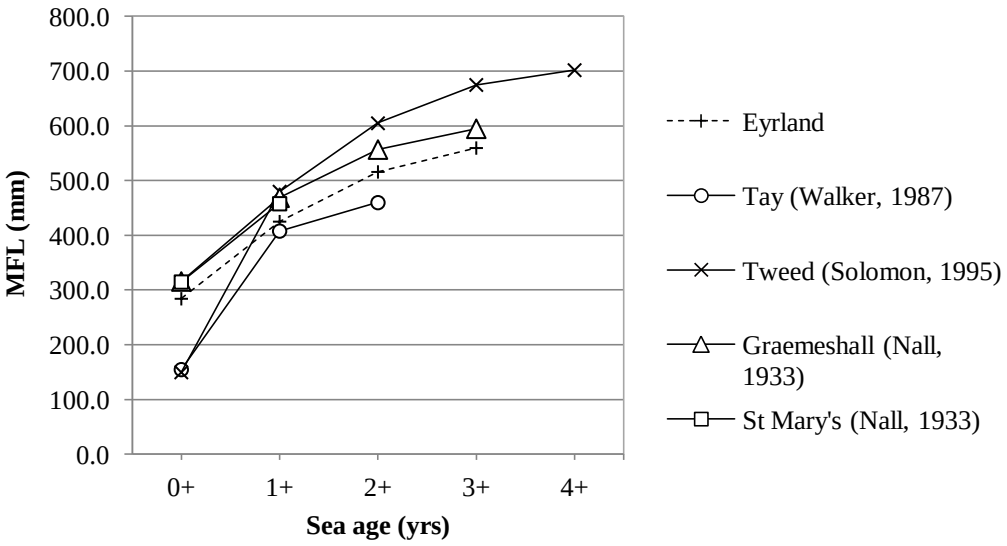


Figure 7.7: Comparison of size at age for sea trout from the Eyrland burn ond other Scottish populations.

Smolt age appeared to have a strong influence on marine growth rates. S1 smolts exhibited the greatest first year marine growth which declined with smolt age. This agreed with findings from other studies (Jonsson & L'Abée-Lund, 1993). Moreover, S1 smolts were able to maintain relatively good growth in their second year at sea, while growth in S2 smolts almost halved. Such a marked decrease in growth rate is commonly associated with the onset of maturity (Jonsson, 1985). Smolts which are younger and smaller on entering the sea generally take longer to reach maturity and therefore can maintain higher growth for longer than older larger smolts (Jonsson & L'Abée-Lund, 1993). However, in this case it was interesting to note that all S1 smolts which were sampled at a sea age of 1+ or 2+ were mature. This suggests that the relatively fast growth exhibited by S1 smolts in freshwater is carried through to their marine growth phase, *i.e.* they are inherently faster growing, whatever their state of sexual development.

However, consideration should again be given to B-growth and the impact this might have on the estimation of marine growth. All of the studies referred to above estimated marine growth by back calculation, and invariably take the start point for marine growth to be the end of the last freshwater winter annulus. In that case, any B-growth is excluded and the risk exists that first year marine growth is over-estimated. In this study, it was possible to adjust the rates of marine growth calculated here by deducting

Table 7.9: Marine growth increments in sea trout returning to the Eyrland Burn, 2007 & 2009. First year growth is adjusted for B-growth.

Smolt age	1st year growth (mm)	Mean B-growth (mm)	1st year growth, adjusted (mm)	2nd year growth (mm)	3rd year growth (mm)
1	196.2	37.5	158.7	140.1	-
2	184.7	17.6	167.1	85.2	80.3
3	160.4	9.1	151.3	-	-

the mean B-growth achieved by each age cohort of smolts calculated from smolt trap data for the Eyrland population (detailed in Chapter 6). This adjustment is shown in Table 7.9. The adjusted marine growth was reduced in all age cohorts but particularly in the youngest age cohorts. The range in first year marine growth exhibited by the different age cohorts decreased from 36mm to 16mm and S2 smolts showed marginally greater growth than the other two age cohorts. This contrasts with observations made previously that marine growth tends to be fastest in the youngest smolt cohorts (Jonsson & L'Abée-Lund, 1993; Nicieza & Braña, 1993; Pratten & Shearer, 1983b). In this case, first year marine growth was similar across the age range, which reflects the work of Friedland *et al.* (2006) who found no relationship between smolt size and first year marine growth rate. This finding also suggests that the fastest growing smolts in freshwater, *i.e.* S1s, are not necessarily the fastest growing at sea. However, it should be recalled that S1 smolts were able to maintain good second year growth at sea while other age cohorts exhibited significantly reduced growth.

Survival

The return rate of finnock to the Eyrland burn was relatively low at approximately 4% in both years. Low rates have been reported elsewhere, *e.g.* in France (Euzenat *et al.*, 1999) and in such cases, return rates for older fish are higher. The conclusion to draw from this is that here and elsewhere, most finnock do not return to spawn after their first summer at sea, although they are well known to move between freshwater and the sea in their natal or neighbouring streams (Euzenat *et al.*, 1999; Pratten & Shearer, 1983b). It was noted previously in Chapter 3 that lone finnock were found in three other Orkney burns which otherwise supported no trout, exemplifying their capacity to wander between different freshwater systems. The return rate for 1+ fish to the Eyrland burn in 2009 was much higher (19.1%) and represents a better measure of marine survival in

this population. While this is very close to the estimated 21.7% survival rate for 1+ sea trout in the River Bresle, Normandy (Euzenat *et al.*, 2006) it is very likely that rates will vary widely between rivers and between years, depending on local growth conditions in freshwater and the sea.

In conclusion, the data presented in this Chapter provide a detailed account of the return migration of sea trout to the Eyrland burn. Through an effectively operated upstream trap it was possible to count returning sea trout and collect information on fish size, age and sex, as well as the seasonal timing of their return and the factors which influenced upstream movement. This showed that sea trout mainly returned to the burn in October, moved upstream during or shortly after increases in water level and were comprised mainly of females, aged 1+ and 2+ (sea winters). Smolt age in returning fish closely reflected that of outgoing smolts, *i.e.* were mostly S2s. The back calculated smolt size of fish underestimated empirically observed S1 smolts size in this population, unless B-growth, also estimated empirically, was included. Marine growth rates fell within the range published for other populations. Fish which had smolted younger initially appeared to have grown faster at sea than older smolting fish. However, when these estimates were adjusted to account for B-growth, the difference in growth rates between fish of different smolt age was reduced and S2 smolts, rather than S1s, exhibited marginally highest marine growth. This highlights the important role of B-growth in the study of smolt size and marine growth.

CHAPTER 8: CONCLUSIONS

8.1 Introduction

G.H Nall commented that an examination of Orkney's sea trout would provide "a *valuable addition to our knowledge"* (Nall, 1930). This final chapter reviews the work undertaken during this project and highlights the key findings with respect to the aims described in Chapter 1. Those aims were partly derived from the 2004 Cardiff conference on sea trout which identified additional research themes in relation to the migratory habits of sea trout, specifically in relation to environmental and genetic controls, stock recruitment processes in different stream types and life history strategies in different geographic regions (Milner *et al.*, 2006). This project addressed those research themes directly through investigation of environmental factors and stock structures in very small catchments in a poorly studied geographic area. This chapter considers the findings and their significance in developing the scientific understanding of anadromous brown trout ecology. The main findings of this thesis can be summarized as follows.

The first phase of work (Chapter 3) required a broad approach to provide the platform from which more targeted investigations could be launched. A total of 36 separate brown trout populations were identified that comprised fish aged up to 5+ years old. Those results alone were of significant local value, which is discussed later, but they also suggested a degree of variation in certain key characteristics between different populations, such as freshwater growth and smolt age. An important aspect of subsequent investigations was the ability to access faster and slower growing populations from separate catchments in close proximity (<10km), owing to the unique geology of the Orkney Islands. Smolts were aged between one and four years old although MSA was lower in faster growing populations. B-growth was evident in smolts. More detailed examination of four populations (Chapter 4) successfully contrasted freshwater growth patterns in trout populations on the Orkney mainland and the island of Hoy. Hoy trout were significantly slower growing. Density did not influence growth rate within or between the four populations. While stream size had a direct effect on the incidence of mature male trout, it did not influence growth in any of the study populations, which instead was linked to an unexpected temperature difference between the four closely neighbouring burns. The subsequent investigation

of smolt characteristics in the same four populations (Chapter 5) found that trout which grew faster in freshwater smolted at a younger age. Smolts from the mainland burns grew faster and therefore smolted at a younger age on average than smolts from the Hoy burns. Between the four populations, mean smolt size varied directly with stream size. B-growth had a significant effect on smolt size by the time of seawater entry, particularly in the youngest smolts. Perhaps more interestingly, among same aged individuals, the smallest trout achieved the greatest B-growth. A more in depth analysis of smolts produced from the Eyrland burn on the Orkney mainland (Chapter 6) highlighted a possible lunar influence on downstream smolt migration and evidence of de-smolting one year followed by re-smolting the following year. Strong evidence of an inverse relationship between smolt size and the expression of B-growth was found among same aged individuals. Supporting evidence was presented for a target smolt size in this population of 130mm at seawater entry. Finally a study of sea trout returning to spawn in the Eyrland burn (Chapter 7) revealed that females were more numerous, older and larger on average than returning males. An approximate marine survival rate was estimated. B-growth also played an important role in the estimation of both smolt size and marine growth rate using scales from returning sea trout. These findings included several interesting and novel insights into the ecology of anadromous brown trout populations which are reviewed in the following pages.

8.2 Migratory habits

Perhaps the most significant finding made in this thesis related to the migratory habits of sea trout, or more specifically, to growth patterns in smolts of different ages and sizes. B-growth was a strong characteristics of smolts sampled in Orkney. First described in Atlantic salmon (Went, 1939) and then in sea trout (Went 1949), B-growth (or B-type growth), is freshwater growth achieved by smolts in the spring period immediately prior to seawater entry. In this study, B-growth played a significant role in determining smolt size at seawater entry. Mean B-growth was inversely related to smolt age, *i.e.* younger smolts achieved greater B-growth, which has been noted previously (Went, 1949). However, irrespective of age, the fundamental determinant of B-growth appeared to be size (FL) at the end of the last freshwater winter annulus where a strong inverse relationship was observed. The clear trend in B-growth expression between smolts of different age and size highlighted a particularly dynamic aspect of trout growth. Individuals in a population exhibited periods of slow and fast growth relative to their (same aged) counterparts at different stages in their freshwater

development. For example, among S1 smolts, fish which achieved a greater size by the end of their first winter in freshwater exhibited less B-growth in the run up to seawater entry than fish which were smaller at the end of winter. While the general trend remained similar, the absolute extent of B-growth appeared to vary between years. In this case it was found that variation in water temperature between late winter and spring was at least partly responsible for this year to year variation. It is also possible therefore that other environmental parameters which can influence growth rate such as water chemistry, water flow, habitat and food availability could also affect B-growth between years, although no data were available to test these hypotheses. Therefore, while a genetic component to this aspect of growth could not be ascertained, it was shown that environmental conditions played a part in the expression of B-growth, which in turn affected smolt characteristics at a crucial moment in the sea trout's life history.

Whatever the fine controls, B-growth represented a significant stage in smolt development and it was clear in the case of the Eyrland population that B-growth occurred in freshwater, immediately before sea entry. This aspect of freshwater growth necessitates a review of some traditional concepts and research methodologies concerning *Salmo trutta*. Firstly, it has been proposed by some authors that migration in brown trout is stimulated by growth restriction and that individuals with a faster metabolism migrate at a younger age as they reach these growth "bottlenecks" sooner than individuals with a slower metabolism (Forseth *et al.*, 1999). This appears to conflict with findings in this study which demonstrated that S1 smolts exhibited significantly more B-growth than older cohorts. How are they able to achieve so much B-growth if their growth in freshwater is being restricted? If they are able to attain fast growth why don't they stay in freshwater or is B-growth a specific component of the smoltification process and stimulated/affected by hormonal changes? A question also remains about the moment when an individual fish diverges from the path of residency and begins the smoltification process. In Atlantic salmon it is thought that smoltification is initiated by decreasing day length the previous autumn among fish which have reached a certain size threshold, resulting in a bi-modal size distribution comprising non-smolting (lower mode) and smolting (upper mode) fish (Heggenes & Metcalfe, 1991). While Nielsen *et al.* (2003) suggested that brown trout follow a similar pattern to Atlantic salmon, autumn bi-modality was not observed in any of the populations studied here (see Chapter 4) which suggests that the smoltification process differs to some extent between the two species. However, Nielsen *et al.* (2003) did find

that in a wild brown trout the expression of Na^+,K^+-ATPase enzyme in gill chloride cells started to increase among smolting individuals from late February onwards. This suggests that smoltification is certainly in progress by that time period and assuming a similar situation in the populations studied here, it is likely that B-growth occurred concurrent to the smolting process. However, many other physiological and biochemical processes occur during smoltification. Stefansson *et al.* (2008) provide an excellent review of these in relation to Atlantic salmon and should give some clues as to potential controls or initiators of B-growth in brown trout smolts. The role of growth hormone, considering the physiological changes which it stimulates, *e.g.* tissue remodeling (length rather than weight increase) and increased food intake, could form one line of inquiry.

8.2.1 B-growth – implications for research (past, present & future)

The B-growth data also suggest a fresh look at studies which employ scale reading methodologies to estimate smolt size or marine growth. A surprisingly small number of studies appear to acknowledge the presence of B-growth in anadromous *Salmo trutta* (Fahy, 1981; Pratten & Shearer, 1983a) and a strong argument is presented here that in fact none have properly accounted for the significance of B-growth. Widely used scale reading methodologies such as those described by Lea (1910), Jonsson & Stenseth (1976) and Elliott & Chambers (1996) infer that the passage of a smolt to the sea occurs at the moment between the final winter growth check in freshwater and the beginning of a rapid (marine) growth phase. Back-calculation therefore estimates smolt size at the end of the last winter annulus in freshwater. This study has shown that this is not necessarily the case as rapid B-growth may occur in freshwater prior to sea entry. Therefore, studies which involve back calculation of smolt size using traditional scale reading methods risk mis-identifying the moment that a smolt enters the sea, with two potential repercussions.

Firstly, smolt size might be underestimated, particularly in cases involving the youngest smolt cohorts, which appear to show the greatest B-growth on average. A good example of this was provided in Chapter 7, which examined mature sea trout from the Eyrland population. Among fish which had smolted at age one, mean size at the end of the last freshwater annulus was 114.5mm. However in Chapter 5 the mean size of S1 smolts sampled in the downstream trap between 2004 and 2010, *i.e.* at the moment of

seawater entry, was 144.5mm (26% greater than the back-calculated estimate). Jonsson *et al.* (2001) recorded a mean smolt size of 6-8cm in two populations which appears to be well below the average shown by other European populations (Jonsson & L'Abee-Lund, 1993). In the present study, many S1 smolts were estimated to be around 8cm at the end of winter, but after B-growth, almost all were larger than 130mm by the time of seawater entry with a mean size of over 140mm.

Secondly, the failure to account for B-growth could result in the overestimation of marine growth rates if it assumed that the marine growth periods begins at the end of the last freshwater winter. Such a study includes that by L'Abée-Lund *et al.* (1989) which estimated first summer marine growth in 34 populations across Norway and used the back-calculation method of Lea (1910). In this study, marine growth rates initially suggested that the youngest smolt cohorts (S1s) grew fastest over their first summer at sea, as found elsewhere (Jonsson & L'Abée-Lund, 1993; Nicieza & Braña, 1993; Pratten & Shearer, 1983). However, when marine growth rates were adjusted for B-growth, it was found that marine growth rates became similar in each smolt age cohort, with S2 smolts showing marginally greater growth. Which is the most relevant point (end of winter or seawater entry) in terms of smolt development? Both moments are clearly important, but given that traits such as osmoregulatory ability and predator avoidance improve with size (Hoar, 1988; Dieperink *et al*., 2002), then the time at which smolts enter the sea would seem to be the point where knowledge of size would be most desirable. Therefore, it seems crucial that B-growth is properly accounted for in ongoing and future research on anadromous brown trout, particularly in populations that produce young and/or small smolts, such as those in southern Europe or those inhabiting very small systems. However, there are major difficulties with this, not least the requirement to distinguish between B-growth (freshwater) and marine growth in the scale reading process.

8.2.2 B-growth – a threshold smolt size for seawater entry?

The B-growth results also were highly relevant to the threshold smolt size debate, where growth has an influence on migratory behaviour. First proposed by Fahy (1985), the hypothesis that brown trout smolt after reaching a threshold size was subsequently rejected by Økland *et al*. (1993). More specifically, the presence of a *universal* size threshold was refuted, based on the fact that in the study population, S3 smolts were

larger on average at age two than S1 smolts, but did not smolt, *i.e.* they were apparently large enough to smolt but failed to do so. That study also employed the scale reading methodology described by Lea (1910) and assumed that smolts moved into seawater immediately after the end of the last freshwater winter. Initially, a similar result was found here, *i.e.* on average, S3 smolts were larger at age two than S1 smolts were at the end of winter. However, S3 smolts at age two were *not* larger than S1 smolts were at seawater entry, due to the S1 size increase achieved via B-growth. This pattern was evident in all four populations studied here. This contrasts with the findings of Økland *et al*. (1993), and supports the hypothesis of a threshold size in anadromous brown trout originally proposed by Fahy (1985).

In the Eyrland burn, the vast majority of fish were greater than 130mm in size by the point of seawater entry, *i.e.* after the B-growth phase. This hypothesis was contradicted by a small number of S3 smolts which were larger than 130mm at age two. It should be noted that the number of larger fish which failed to smolt at the putative threshold size comprised only 24 fish out of approximately 2400 smolts collected over the sampling period. This number was reduced to 18 when so called "repeat" smolts were excluded. Further information on the frequency of repeat smolts would be desirable, especially among large S3 smolts. A similar analysis between S1 and S3 smolts in other populations where data is available is also warranted.

8.2.3 Repeat smolts

The occurrence of repeat smolts, *i.e.* smolts which de-smolted one year but survived and re-smolted the following year, was a novel finding and adds further to our knowledge of the migratory habits of *Salmo trutta*. No evidence of this phenomenon in wild salmonids could be found in the literature, although it has been demonstrated experimentally in Atlantic salmon (Eriksson, 1984; Shrimpton *et al*., 2000). It is thought that desmolting occurs when smolts are delayed in their downstream passage long enough to lose the necessary pre-adaptations for the transition into saltwater (Björnsson & Bradley, 2007; Stefansson *et al*., 2008). Desmolting may also be promoted by increasing water temperatures (Soivio *et al*., 1988; Kurokawa, 1990). Those studies highlighted the potential consequences of obstructions and/or delays to the downstream passage of smolts. This may be caused by low water conditions, seen in this study in 2008, when water levels were very low and the smolt run was delayed

by approximately one month. However, similar behaviour was also noted in 2009, when water levels were consistently high and there was no apparent delay to the smolt run. Man made dams and weirs may also hinder downstream progress although, somewhat ironically, they also make excellent fish trapping locations which in turn provide excellent data on migratory behaviour in salmonids! Fish trapping and handling also represents a potential stressor for downstream moving smolts (Pickering *et al.*, 1982; Iversen *et al.*, 1998) and therefore may have to some extent contributed to the de-smoltification observed here. Clearly it would be possible to study this phenomenon in other systems where smolt trapping is carried out routinely.

In light of the discussion in the previous section, an alternative theory could be proposed that desmolting occurs in fish which initially begin to smolt but fail to reach the threshold size of 130mm within the right time frame. This would explain why desmolting occurred in years where there was no apparent delay to downstream migration. While the apparent recapture rate of repeat smolts was very similar in each case (around 26% of smolts released upstream desmolted in each year and were recaptured as smolts the following year), the numbers involved were relatively low and a more specific sampling methodology would be required to determine the rate of de-smolting, the rate of survival to re-smolt the following year and the causes of this phenomenon. Further research on the subject is clearly warranted to measure the possible impact of this behaviour on smolt production.

8.3 Stock recruitment

The second area identified as a research need related to stock recruitment processes in different stream types. The work carried out on the Eyrland burn allowed approximate estimates of stock recruitment in a relatively small stream which is typical of those through Orkney and other Scottish Islands. To the author's knowledge, it is the first instance of such data being available for a stream of this size and type in the UK, particularly considering that it supports only wild brown trout, in contrast to other systems where trout are sympatric with salmon (Tournaig, North Esk) or are artificially stocked (Shieldaig). The upstream trap used here provided data on the size of the spawning population, from which egg deposition could be estimated. Annual egg deposition varied between approximately 100,000 and 130,000, according to the model of Elliott (1984). This resulted in an autumn fry density of approximately 15-40

fish/100m^2 and a smolt production of around 500-600 (S1, S2 and S3 smolts) per egg cohort, providing an approximate survival rate for egg to smolt of 0.42%. Smolt production in terms of the wet area varied from 2 – 5 per 100m^2 wet area, which was within the range estimated in other studies, *i.e.* 1.2 – 19.8 smolts per 100m^2 (Hesthagen *et al*., 1986; Rasmussen, 1986). However, as noted previously, few published estimates exist for systems which support wild brown trout only. Recruitment from the smolt stage to the spawning population could also be estimated for the Eyrland population. Survival rates for finnock were relatively low at 4% and it was suggested that many fish of that age do not return to the burn after their first summer at sea. This was supported by the much higher return rate for 1SW sea trout of approximately 20%.

Fewer data were available from the other three burns in this study, although those collected could be compared to Eyrland. Population structure for example was clearly different in the Hoy burns and therefore rates of recruitment were liable to be different also. The density of juvenile fish was lower, growth rates were lower and smolt age was high, relative to the Eyrland population. Therefore, it could be speculated that smolt production in the Hoy burns might be lower than observed in the Eyrland burn. In the Bu burn, while the density of juvenile fish was high, these mainly comprised 0+ fish and the production of older fish was apparently depressed, relative to the Eyrland burn. This was possibly due to its size, being the smallest of the study group. Mean smolt size (all ages) was also the smallest in the Bu population, as it produced a larger number of younger smolts (S1s) than the other burns. This may have implications for marine survival, the rate of which has been directly related to smolt size (Hoar, 1976). Considering also that the Bu has a relatively small area of productive freshwater habitat, it is reasonable to assume that smolt production here would be considerably less than that seen in the Eyrland burn for example. It follows that with a potentially reduced rate of marine survival, due to the smaller smolt size, then the size of the spawning population may also be far lower than that of Eyrland, which comprised around 80 females in 2009. In terms of conservation this highlights the fragility of small populations such as that inhabiting the Bu. Hazards include drought, pollution, predation, parasite infections and reduced food availability. Another issue to consider is angling pressure and clearly a population which is sustained by a relatively small number of females is more at risk from over-exploitation. It is easily possible that the actions of even one angler could have a major impact on the egg deposition in small burns like the Bu when it is likely that the spawning population may only comprise a

few dozen females at most. It certainly highlights the need for restraint to be shown by anglers, particularly in the latter part of the season. Clearly much of this is speculative but highlights the need to ascertain smolt output and spawning population size in other brown trout populations in Orkney.

8.4 Life history strategies

The third and final research theme involved the investigation of life history strategies in different geographic regions. This aim was clearly met as this project represents the most extensive (and intensive) study of anadromous brown trout populations ever undertaken in the Orkney Islands. Life history strategies among the populations studied in detail appeared to be broadly similar to that seen in other regions (Jonsson, 1985; Forseth *et al.*, 1999; Jonsson *et al.*, 2001; Campbell, 1977). For example, among the four populations studied in detail, trout which remained resident and matured in freshwater were almost exclusively male, while the upstream trap at the Eyrland burn revealed that most returning sea trout were female. It is likely that this is the case in most of Orkney's small coastal burns but it would be interesting to determine whether the same is true in Orkney's larger lochs systems which also have sea access, *e.g.* the Loch of Harray. Fidelity to the natal stream was also demonstrated but less than half of the sea trout returning to the Eyrland burn bore marks/tags applied at smolting. This suggested that some straying occurs, although it was not possible to estimate its frequency.

The findings on B-growth dynamics and de/re smolting are also novel aspects of the sea trout's life history to be revealed in this thesis. It is argued that greater consideration of this aspect of growth should be given to the study of anadromous brown trout in general. It was possible to study the effect of freshwater growth rate on migratory activity both within and between populations. Within each of the four populations studied in detail, fish which migrated to sea comprised both the fastest and slowest growing individuals in the population, *i.e.* the youngest and oldest smolt age cohorts, respectively. Fish which matured in freshwater exhibited an intermediate rate of growth within the range exhibited by their migratory counterparts, which underpins similar observations made in Norway (Jonsson, 1985). This trend also reflects the hypothesis that multiple and also fits with the hypothesis proposed for Atlantic salmon, where multiple thresholds apply at different stages in the development pathway which end in

either migration to sea via a fast (young smolts) and slow (old smolts) growth trajectories, or freshwater residency and maturity, via an intermediate growth trajectory maturity (Paez *et al*., 2011; Rossignol *et al*., 2011). In these instances, absolute growth rate did not appear to determine whether fish smolted and migrated to sea or remained in freshwater and matured. This suggests an element of genetic programming in these fish – migration is inevitable, the only uncertainty lies in the age that it occurs and this is the element which is most likely determined by an individual's growth and/or metabolic rate. This apparent "hard-wiring" was further demonstrated by repeat smolts, which pursued a migratory life history even when delayed in freshwater by an additional year. All of these observations could be used as evidence of alternative migratory tactics, described in salmonid populations by Dodson *et al*. (2013).

Variation in freshwater growth between populations was also evident and had knock-on life history effects. The slower growing trout in the two Hoy populations smolted at an older age compared to the faster growing mainland populations. Variation in latitude, which is reported to influence characteristics such as smolt age (Jonsson & L'Abée-Lund, 1993), was effectively ruled out as a factor here as all four study populations were located with a few miles of each other. Despite this however, it was found that water temperature varied significantly between the four burns, presumably due to variation in stream size, aspect and groundwater inputs between the four catchments. It was found that the variation in water temperature as well as stream size had a significant effect on parameters characteristics such as freshwater growth rate, the incidence and size of mature resident males, smolt age and smolt size. While they may be more important in a local context, it would also be necessary to consider the role of environmental conditions in freshwater when comparing populations across larger geographic areas to accurately determine the influence of changing latitude on life-history characteristics in anadromous brown trout.

8.5 Local relevance of this work

Aside from scientific objectives, the other motivation for undertaking this work was to determine the status of sea trout populations in Orkney, given the dearth of information which existed previously and the apparent decline in sea trout catches in the early 2000s. It is now known with some confidence exactly which watercourses in Orkney

support trout populations and which of those show anadromous behaviour. This is of major significance as it can be fed into the local planning system so that for the first time, cognizance can be taken of the presence of trout populations in relation to local developments. Past developments can also be targeted, for example, under the Water Framework Directive, through which SEPA is working to remove barriers, such as dams and culverts, to both the upstream and downstream passage of migratory fish. Priority should clearly be given to those systems where trout are known to be present, with information now available across Orkney. Habitat projects, such as the one carried out at the Bu burn in 2007 with funding support from the Wild Trout Trust and the Scapa Flow Landscape Partnership (led by the author) can now target appropriate sites. Knowledge of the burns which don't currently support trout is also a useful baseline for future projects, such as habitat improvement and establishment of trout populations. However, since this work started in 2004 there is a need to re-survey many of the sites sampled in this thesis to provide up to date information on the distribution and health of trout populations in Orkney.

On the subject of ongoing monitoring work, a number of benchmarks have been set. A network of electrofishing survey sites now exist across Orkney, comprising three-run, fully quantitative sites on a number of brown and sea trout spawning burns and single run (timed) sites on the four sea trout burns on the mainland and Hoy. The work at the Eyrland burn has also provided benchmarks on smolt production and spawning population size through the operation of downstream and upstream trapping facilities. These all provide a range of opportunities in an area which has proven itself as an excellent venue for research into anadromous trout ecology. In freshwater, the downstream migration of smolts in the absence of obstructions would make an interesting comparison to Eyrland trap data and could either be achieved by sampling further upstream in the Eyrland burn or in a different system entirely. A better understanding of the de-smoltification and re-smoltification process would also be of interest. In the marine phase, tagging work would provide information on smolt movements and rates of fidelity/straying. Sampling for marine parasites, *e.g.* the salmon louse, *Lepophtheirus salmonis*, would also provide valuable data which would complement similar work occurring on the west coast of Scotland. One obvious line of inquiry not addressed in this project was the brown trout population inhabiting Orkney's largest watercourse, the Loch of Harray and the linked Loch of Stenness. This system has numerous spawning burns and provides a unique range of habitats comprising a

large freshwater loch (Harray) which is extremely productive in terms of its (resident) brown trout population and similarly sized brackish loch (Stenness) which appears to sustain a much smaller resident trout population (Duncan *et al.*, 1992). Angling records indicate that sea trout are caught in both lochs and it is thought that they spawn in the burns there too. Given the area of available habitat, in an Orkney context these lochs represent a potentially significant source of sea trout, although the urge to migrate to sea may be tempered by the apparently productive conditions in freshwater. Numerous lines of inquiry spring to mind and unquestionably it would be useful to know more about the trout inhabiting this unusual system. However, its size presents the type of sampling challenges which are common to all large systems and perhaps only serve to highlight the attractiveness of Orkney's smaller burns as venues for sea trout research. Ultimately, such work must be resourced and the absence of a fishery trust or DSFB in Orkney represents a major obstacle to future survey work on brown trout populations in Orkney.

8.6 Summary

This study has revealed the distribution of sea trout populations in small systems across Orkney. It has provided novel insights into freshwater growth and behavioral patterns in anadromous individuals. Among smolts, B-growth was found to occur in freshwater and caused significant size increase in the period between the end of winter and seawater entry. Expression of B-growth in smolts was inversely related to size at the end of winter before migration, with the result that smaller smolts were able to partially catch up in terms of size with larger smolts by the time of seawater entry. Interestingly, B-growth is rarely accounted for in the existing literature on sea trout. In studies which involve back calculation of growth history using scale samples taken from adult sea trout, there is a risk that smolt size and first year marine growth rates are underestimated if B-growth is not taken into account. The B-growth data also refreshes the debate about the presence of a threshold size in sea trout smolts. In this study it was shown that the vast majority of smolts in the Eyrland population had reached or exceeded 130mm by the moment of seawater entry. The occurrence of repeat smolts, *i.e.* fish which de-smolted, remained in freshwater and smolted again the following year, has not been observed previously in any wild salmonid population. Information on stock recruitment (particularly in the Eyrland burn) and life history strategies was also obtained which were novel in two main aspects. All of the catchments surveyed were

small in terms of both geographic extent and discharge, providing data for sea trout from a type of water-course not previously studied in detail in the UK. The data also relate to sea trout populations which exist in isolation from other salmonid populations, *e.g.* Atlantic salmon. Life history strategies among Orkney populations of sea trout exhibited some similarities to other populations, *e.g.* the tendency for males to reside and mature in freshwater and for females to smolt and migrate to sea. However, the findings in relation to B-growth and de/re-smoltification were novel. The latter behaviour suggests that some fish at least seem "hard-wired" for a migratory lifestyle. This was further demonstrated by the observation that within populations, absolute growth rate did not determine the choice of lifestyle (resident or migratory), with fish which matured in freshwater exhibiting a growth rate which was within the range shown by fish that smolted. The data also showed that in the absence of a latitudinal effect, environmental conditions such as stream size had a significant effect on life history traits.

It is the hope of the author that this study represents the "*valuable addition to our knowledge"* predicted by Nall (1930). In a local context it has provided, for the first time, the information necessary for effective conservation of brown trout populations in Orkney. In a modern scientific context it has highlighted previously unreported aspects of anadromous brown trout ecology, such as the relationship between initial size and B-growth and the occurrence of repeat smolts. An extension of the methods employed in this thesis to other anadromous trout populations would help to better understand these characteristics. This study has highlighted the value of small streams and the relative ease with which a large proportion of the populations can be sampled. A natural progression would be to study these characteristics in populations inhabiting small streams elsewhere, but it would also be necessary to study how these characteristics vary with stream size and geographically, across the native range of the brown trout.

References

Alabaster, J. S. & Lloyd, R., 1982. Water Quality Criteria for Freshwater Fish. London: Butterworths.

Alm, G., 1950. The sea trout population in the Ava stream, Drottningholm: Institute of Freshwater Research.

Armstrong, J. D., Gardiner, W. R. & Walker, A. F., 1994. Juvenile brown trout production in the Loch Leven catchment. Fisheries Research Services Report No. 7/94. Faskally, Pitlochry, Perthshire: Scottish Office Agriculture and Fisheries Department.

Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M. & Milner, N.J., 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fisheries Research, Volume 62, pp. 143–70.

AST, 2011. Sea trout workshop 9th and 10th February 2011, Plas Menai, Bangor. Perth, Atlantic Salmon Trust.

Aubin-Horth, N. & Dodson, J.J., 2009. Influence of individual body size and variable thresholds on the incidence of a sneaker male reproductive tactic in Atlantic salmon. Evolution, Volume 58 (1), pp. 136-144.

Ayrshire Rivers Trust, 2010. River Ayr Smolt Trap 2010. Auchincruive, Ayr: Ayrshire Rivers Trust.

Backeil, T. & Le Cren, E. D., 1978. Some density relationships for fish population parameters. In: S. D. Gerking, ed. Ecology of Freshwater Fish Production. Oxford: Blackwell Scientific Publications, pp. 279-302.

Baglinière, J. L. & Maisse, G., 1985. Precocious maturation and smoltification in wild Atlantic salmon in the Armorican massif, France. Aquaculture, 45(1), pp. 249-263.

Baker, R.R., 1978. The Evolutionary Ecology of Animal Migration. London: Hodder & Stoughton. 1012 pp.

Behnke, R.J., 1986. Brown trout. Trout, Volume 27, pp. 42‑7.

Bennion H., Hilton J., Hughes M., Clark J., Hornby D., Kernan M. & Simpson G., 2002. Development of a risk based prioritisation protocol for standing waters in Great

Britain based on a georeferenced inventory – Phase 2. Environment Agency R&D Technical Report P2-260/2/TR1.

Berg, O. K. & Jonsson, B., 1990. Growth and survival rates of the anadromous trout, *Salmo trutta*, from the Vardnes River, northern Norway. Environmental Biology of Fishes, Volume 29, pp. 145-154.

Berry, R. J., 1985. The Natural History of Orkney. Glasgow: Collins.

Berthold, P., 1991. Genetic control of migratory behaviour in birds. Trends in Ecology and Evolution. Volume 6, pp. 254–7.

Biebach, H., 1983. Genetic determination of partial migration in the European robin (*Erithacus rubecula*). Auk, Volume 100, pp. 601–6.

Bjornsson, B. T. & Bradley, T. M., 2007. Epilogue: past successes, present misconceptions and future milestones in salmon smoltification research. Aquaculture, Volume 273, pp. 384-391.

Boeuf, G., 1993. Salmonid smolting: a pre-adaptation to the oceanic environment. In: J. C. Rankin & F. B. Jensen, eds. Fish Ecophysiology. London: Chapman & Hall, pp. 105-135.

Bohlin, T., Dellefors, C. & Faremo, U., 1993. Optimal Time and Size for Smolt Migration in Wild Sea Trout (*Salmo trutta*). Canadian Journal for Fisheries and Aquatic Sciences, 50(2), pp. 224-232.

Bohlin, T., Dellefors, C. & Faremo, U., 1994. Probability of first sexual maturation of male parr in wild sea-run brown trout (*Salmo trutta*) depends on condition factor 1 yr in advance. Canadian Journal of Fisheries and Aquatic Sciences, Volume 51, pp. 1920-1926.

Bohlin, T., Dellefors, C. & Faremo, U., 1996. Date of smolt migration depends on body-size but not age in wild sea-run brown trout. Journal of Fish Biology, 49 (1), pp. 157–164.

Bohlin, T., Pettersson, J. & Degerman, E., 2001. Population density of migratory and resident brown trout (*Salmo trutta*) in relation to altitude: evidence for a migration cost. Journal of Animal Ecology, Volume 70, pp. 112-121.

Borgstrøm, R. & Heggenes, J., 1988. Smoltification of sea trout (*Salmo trutta*) at short length as an adaptation to extremely low summer stream flow. Polish Archives of Hydrobiology, Volume 35, pp. 375-384.

Butler, J., 2002. River Ewe Fishery Management Plan 2002 - 2006. A report by the Wester Ross Fisheries Trust.

Butler, J. R. A. & Walker, A. F., 2006. Characteristics of the Sea trout (*Salmo trutta* L.) Stock Collapse in the River Ewe (Wester Ross, Scotland). In: G. S. Harris & N. J. Milner, eds. Sea Trout: Biology, Conservation and Management. Proceedings of the First International Sea Trout Symposium, Cardiff, July 2004. Oxford: Blackwell Publishing Ltd, pp. 45-59.

Björnsson, B. T. & Bradley, T. M., 2007. Epilogue: Past successes, present misconceptions and future milestones in salmon smoltification research. Aquaculture, 273 (2–3), pp. 384–391.

Byrne, C. J., Poole, R., Dillane, M., Rogan, G. & Whelan, K.F., 2004. Temporal and environmental influences on the variation in sea trout (*Salmo trutta* L.) smolt migration in the Burrishoole system in the west of Ireland from 1971 - 2000. Fisheries Research, Volume 66, pp. 85-94.

Caballero, P., Cobo, F. & Gonzalez, M. A., 2006. Life History of a Sea Trout (Salmo trutta L.) Population from the North-West Iberian Peninsula (River Ulla, Galicia, Spain). In: G. Harris & N. Milner, eds. ea Trout: Biology, Conservation and Management. Proceedings of First International Sea Trout Symposium, Cardiff, July 2004. Oxford: Blackwell Publishing, pp. 234-247.

Campbell, J. S., 1977. Spawning characteristics of brown trout and sea trout *Salmo trutta* L. in the Kirk Burn, River Tweed. Journal of Fish Biology, Volume 11, pp. 217-229.

Charles, K., Roussel, J.-M., Cunjak, R. A., 2004. Estimating the contribution of sympatric anadromous and freshwater resident brown trout to juvenile production. Marine and Freshwater Research, 55(2), pp. 185–191.

Charter, E. & van Houten, A., 1986. Survey of Orkney Lochs. Peterborough: Nature Conservancy Council.

Cowx, I. G., 1983. Review of the methods for estimating fish population size from survey removal data. Fisheries Management, 14(2), pp. 67-81.

Crisp, D. T., 1981. A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. Freshwater Biology, Volume 1981, pp. 361-368.

Crisp, D. T., 1989. Some impacts of human activities on trout. Freshwater Biology, Volume 21, pp. 21-33.

Crisp, D. T., 2000. Trout and Salmon: Ecology, Conservation and Management. Cambridge: Blackwell Science.

Cucherousset, J, Ombredane, D., Charles, K., Marchand, F. & Baglinière, J. –L., 2005. A continuum of life history tactics in a brown trout (*Salmo trutta*) population. Canadian Journal of Fisheries and Aquatic Sciences, Volume 62, pp. 1600-1610.

Davis, J. C., 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. Journal of the Fisheries Research Board of Canada, Volume 32, pp. 2295-2332.

Dellefors, C. & Faremo, U., 1988. Early sexual maturation in males of wild sea trout, *Salmo trutta* L., inhibits smoltification. Journal of Fish Biology, Volume 33, pp. 741-749.

Dieperink, C., Bak, B. D., Pedersen, L. –F., Pedersen, M. I. & Pedersen, S., 2002. Predation on Atlantic salmon and sea trout during their first days as post smolts. Journal of Fish Biology, Volume 61, pp. 848-852.

Dodson, J.J., Aubin-Horth, N., Theriault, V., Paez, D.J., 2013. The evolutionary ecology of alternative migratory tactics in salmonid fishes. Biological Reviews, Volume 88 (3), pp. 602-625.

Duncan, W. M., Sinclair, D. S. & Beveridge, M. C. M., 1992. The Current status and Future Development of Brown Trout Angling on Orkney and its Surrounding Islands. Stirling: Institute of Aquaculture, University of Stirling.

Egglishaw, H. J. & Shackley, P. E., 1977. Growth, survival and production of juvenile salmon and trout in a Scottish stream, 1966-75. Journal of Fish Biology, Volume 11, pp. 647-672.

Elliott, J. A., 1984. Numerical changes and population regulation in young migratory trout *Salmo trutta* in a Lake District stream, 1966-83. Journal of Animal Ecology, Volume 53, pp. 327-350.

Elliott, J. M., 1981. Some aspects of thermal stress on freshwater teleosts. In: A. Pickering, ed. Stress and Fish. London: Academic Press, pp. 209-245.

Elliott, J. M., 1989. Growth and size variation in contrasting populations of trout, *Salmo trutta*: an experimental study on the role of natural selection. Journal of Animal Ecology, Volume 58, pp. 45-58.

Elliott, J. M., 1994. Quantitative ecology and the brown trout. Oxford: Oxford University Press.

Elliott, J. M., 2015. Density-dependent and density-independent growth in a population of juvenile sea-trout, *Salmo trutta*, assessed using long-term data from a small stream in Northwest England. Freshwater Biology, Volume 60(2): pp. 336-346.

Elliott, J. M. & Chambers, S., 1996. A Guide to the Interpretation of Sea Trout Scales. Bristol: National Rivers Authority.

Elson, P. F., 1957. The importance of size in the change from parr to smolt in Atlantic salmon. Canadian Fish Culturist, Volume 21, pp. 1-6.

Emlen, D.J., 2008. The Evolution of Animal Weapons. Annual Review of Ecology, Evolution, and Systematics, Volume 39, pp. 387 – 413.

Eriksson, T., 1984. Adjustments in annual cycles of swimming behaviour in juvenile Baltic salmon in fresh and brackish water. Transactions of the American Fisheries Society, Volume 113, pp. 467–471.

Euzenat, G., Fournel, F. & Fagard, J.-L., 2006. Population Dynamics and Stock recruitment Releationship of Sea Trout in the River Bresle, Upper Normandy, France. In: G. Harris & N. Milner, eds. Sea Trout: Biology, Conservation and Management.

Proceedings of First International Sea Trout Symposium, Cardiff, July 2004. Oxford: Blackwell Publishing Ltd, pp. 307-323.

Euzenat, G., Fournel, F. & Richard, A., 1999. Sea trout (*Salmo trutta* L.) in Normandy and Picardy. In: J. Bagliniere & G. Maisse, eds. Biology and Ecology of the Brown Trout and Sea Trout. Chichester: Praxis Publishing Ltd, pp. 175-203.

Fahy, E., 1979. Performance of the Crumlin sea-trout Fishery, Co. Galway. Irish Fisheries Leaflet No. 101. Dublin: Dept of Agriculture and Fisheries.

Fahy, E., 1980. Sea trout from the Currane Fishery in 1973 and 1974. Irish Fisheries Investigations Series A19. Dublin: Dept of Agriculture and Fisheries.

Fahy, E., 1981. The Beltra Fishery, Co. Mayo and its sea trout, *Salmo trutta*, stocks. Fisheries Bulletin No. 4. Dublin: Dept of Fisheries and Forestry.

Fahy, E., 1985. Cyclic fluctuations in the abundance of sea trout (*Salmo trutta* L.). Archiv fuer Hydrobiologie Supplementband, Volume 3, pp. 404-428.

Fahy, E., 1990. Spring growing period as a regulator of the size of smolt run in trout *(Salmo trutta*). Archive fur Hydrobiologie, 119(3), pp. 325-330.

Fahy, E. & Rudd, R., 1988. The Currane, Co. Kerry, Sea Trout Fishery, 1980-1986. Irish Fisheries Investigations Series A (Freshwater): No. 31. Dublin: Dept of the Marine.

Falconer D.S. & Mackay, T.F.C., 1996. Introduction to quantitative genetics, 4th edn. Harlow, UK: Longman.

Ferguson, A., 2006. Genetics of Sea Trout, with Particular Reference to Britain and Ireland. In: G. S. Harris & N. J. Milner, eds. Sea Trout: Biology, Conservation and Management. Proceedings of the First International Sea Trout Symposium, Cardiff, Wales, UK, July 2004. Oxford: Blackwell Publishing, pp. 157-182.

Finstad, B., Ugedal, O., Damsgard, B. & Mortensen, A., 1998. Seawater tolerance and downstream migration in hatchery reared and wild brown trout. Aquaculture, Volume 168, pp. 395-405.

Fleming, C.C., 1983. Population biology of anadromous brown trout (*Salmo trutta* L.) in Ireland and Britain. PhD Thesis, The Queen's University of Belfast, 475 pp.

Foote, C.J., 1988. Male mate choice dependent on male size in salmon. Behaviour, Volume 106, pp. 63–80.

Forseth, T., Næsje, T. F., Jonsson, B. & Hårsaker, K., 1999. Juvenile migration in brown trout: a consequence of energetic state. Journal of Animal Ecology, Volume 68, pp. 783-793.

Friedland, K. D., Clarke, L. M., Dutil, J. D. & Salminen, M., 2006. The relationship between smolt and post smolt growth for Atlantic salmon (*Salmo salar*) in the Gulf of St Lawrence. Fishery Bulletin, 104(1), pp. 149-155.

Garcia-Vasquez, E., Moran, P., Martinez, J. L., Perez, J., de Gaudemar, B. & Beall, E., 2001. Alternative mating strategies in Atlantic salmon and brown trout. Journal of Heredity, Volume 92, pp. 146-149.

Gardiner, R. & Shackley, P., 1991. Stock and recruitment and inversely density dependent growth of salmon, *Salmo salar* L., in a Scottish stream. Journal of Fish Biology, Volume 38, pp. 691-696.

Gargan, P. G., Roche, W. K., Forde, G. P. & Ferguson, A., 2006. Characteristics of the Sea Trout (*Salmo trutta* L.) Stocks from the Owenglena and Invermore Fisheries, Connemara, Western Ireland, and Recent Trends in Marine Survival. In: G. S. Harris & N. J. Milner, eds. Sea Trout: Biology, Conservation and Management. Proceedings of the First International Sea Trout Symposium, July 2004, Cardiff, Wales, UK. Oxford: Blackwell Publishing, pp. 60-75.

Godfrey, J., 2005. Site condition monitoring of Atlantic salmon SACs. Pitlochry: Scottish Fisheries Co-ordination Centre.

Grau, E. G., Dickhoff, W. W. & Folmar, L. C., 1981. Lunar phasing of the thyroxine surge preparatory to seaward migration of salmonid fish. Science, Volume 211, pp. 607-609.

Gross, M. R., Coleman, R. M. & McDowell, R. M., 1988. Aquatic productivity and the evolution of diadromous fish migration. Science, Volume 239, pp. 1291-1293.

Hamor, T. & Garside, E. T., 1975. Regulation of oxygen consumption by incident illumination in embryonated ova of Atlantic salmon Salmo salar L.: Ldh-f as a

phytogeographic marker locus. Comparative Biochemistry and Physiology, Volume 52, pp. 277-280.

Hamor, T. & Garside, E. T., 1976. Developmental rates of embryos of Atlantic salmon, *Salmo salar* L., in response to various levels of temperature, dissolved oxygen and water exchange. Canadian Journal of Zoology, Volume 54, pp. 1912-1917.

Harbinson, C., 1998. Sea trout management. Dissertation submitted for a Master of Science in Marine Resource Management. Edinburgh: Heriot Watt University.

Harris, G.. & Milner, N., 2006. Setting the Scene – Sea Trout in England andWales – A Personal Perspective. In: G. S. Harris & N. J. Milner, eds. Sea Trout: Biology, Conservation and Management. Proceedings of the First International Sea Trout Symposium, July 2004, Cardiff, Wales, UK. Oxford: Blackwell Publishing, pp. 1-8.

Heggenes, J. & Metcalfe, N. B., 1991. Bimodal size distributions in wild juvenile Atlantic salmon populations and their relationship with age at smolt migration. Journal of Fish Biology, 39(6), pp. 905-907.

Heidarsson, T., Antonsson, T. & Snorrason, S. S., 2006. The relationship between body and scale growth proportions and validation of two back-calculation methods using individually tagged and recaptured wild Atlantic salmon. Transactions of the American Fisheries Society, 135(5), pp. 1156-1164.

HELCOM, 2011. Sea Trout and Salmon Populations and Rivers in Denmark - HELCOM Assessment of salmon (*Salmo salar*) and sea trout (*Salmo trutta*) populations and habitats in rivers flowing into the Baltic Sea. Balt. Sea Environ. Proc. No. 126A. Helsinki: Helsinki Commission.

Hesthagen, T., Ousdal, J.-O. & Bergheim, A., 1986. Smolt production of Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo salar* L.) in a small Norwegian stream influenced by agricultural activity. Polskie Archiwum Hydrobiologii, Volume 33, pp. 423-432.

Hindar, K., Jonsson, B., Ryman, N. & Stahl, G., 1991. Genetic relationships among landlocked, resident, and anadromous brown trout, Salmo trutta L. Heredity, Volume 66, pp. 83‑91.

Hoar, W. S., 1976. Smolt transformation: evolution, behaviour and physiology. Journal of Fisheries Research Board of Canada, Volume 33, pp. 1233–52.

Hoar, W. S., 1988. The physiology of smolting salmonids. In: W. S. Hoar & D. J. Randall, eds. Fish Physiology. London: Academic Press, pp. 275-343.

Howson, C. M., Steel, L., Carruthers, M. & Gilham, K., 2012. Identification of priority marine features in Scottish territorial waters. Scottish Natural Heritage Commissioned Report No. 388.

Hutchings, J.A., Myers, R.A., 1994. The evolution of alternative mating strategies in variable environments. Evolutionary Ecology, Volume 8, pp. 256–268.

IBIS, 2012. Small streams: contribution to populations of trout and sea trout. Knowledge transfer workshop organised by the IBIS project with the Atlantic Salmon Trust. Glasgow: IBIS.

ICIT (2004). Review of the uses of the lochs and land in the Stenness catchment, Orkney, and associated environmental impacts. Scottish Natural Heritage Commissioned Report No. 066 (Part 10 of 12) (ROAME No. F01LA02).

Iversen, M., Finstad, B. & Nilssen, K. J., 1998. Recovery from loading and transport stress in Atlantic salmon (Salmo salar L.) smolts. Aquaculture, 168(1-4), pp. 387-394.

James, M. A., 2000. Assessing the economic value and realising the potential of recreational freshwater fisheries in the Western Isles. A report prepared for the Western Isles Fisheries Trust. Dunkeld: FRL Ltd.

Jensen, A. J., Finstad, B., Fiske, P., Hvidsten, N. A., Rikardsen, A. H. & Saksgård, L., 2012. Timing of smolt migration in sympatric populations of Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*). Canadian Journal of Fisheries and Aquatic Sciences, 69(4), pp. 711-723.

Jobling, M. & Koskela, J., 1996. Interindividual variations in feeding and growth in rainbow trout during restricted feeding and in a subsequent period of compensatory growth. Journal of Fish Biology, 49(4), pp. 658-667.

Johnson, J.H., McKenna, J.E. & Douglass, K.A., 2013. Movement and feeding ecology of recently emerged steelhead in Lake Ontario tributaries. Journal of Applied Ichthyology, Volume 29 (1): pp. 221-225.

Johnsson, J. I. & Bohlin, T., 2006. The cost of catching up: increased winter mortality following structural growth compensation in the wild. Proceedings of the Royal Society B, Volume 273, pp. 1281-1286.

Johnstone, D.L., O'Connell, M.F., Palstra, F.P. & Ruzzante, D.E., 2013. Mature male parr contribution to the effective size of an anadromous Atlantic salmon (*Salmo salar*) population over 30years. Molecular Ecology, Volume 22(9): pp. 2394-2407.

Jonsson, B., 1982. Diadromous and resident trout *Salmo trutta*: is their difference due to genetics? Oikos, Volume 38, pp. 297-300.

Jonsson, B., 1985. Life history pattern of freshwater resident and sea-run migrant brown trout in Norway. Transactions of the American Fisheries Society, Volume 114, pp. 182-194.

Jonsson, B. & Jonnson, N., 1993. Partial migration: niche shift versus sexual maturation in fishes. Review of Fish Biology and Fisheries, Volume 3, pp. 348-365.

Jonsson, B. & Jonsson, N., 2006. Life History of the Anadromous Trout *Salmo trutta*. In: Sea Trout: Biology, Conservation and Management. Proceedings of the First International Sea Trout Symposium, Cardiff, Wales, UK, July 2004. Oxford: Blackwell Publishing, pp. 196-223.

Jonsson, B., Jonsson, N., Brodtkorb, E. & Ingebrigsten, P.-J., 2001. Life-history traits of brown trout vary with the size of small streams. Functional Ecology, Volume 15, pp. 310-317.

Jonsson, B., Jonsson, N. & Ugedal, O., 2011. Production of juvenile salmonids in small Norwegian streams is affected by agricultural land use. Freshwater Biology, 56(12), pp. 2529-2542.

Jonsson, B. & L'Abée-Lund, J. H., 1993. Latitudinal clines in life-history variables of anadromous brown trout in Europe. Journal of Fish Biology, 43(Supplement A), pp. 1-16.

Jonsson, B., L'Abée-Lund, J. H. & Heggberget, T. G., 1991. Longevity, body size and growth in anadromous brown trout. Canadian Journal of Fisheries and Aquatic Sciences, Volume 48, pp. 1838-1845.

Jonsson, B. & Stenseth, N. C., 1976. Regression of body length on scale size of brown trout, *Salmo trutta* (L.). Norwegian Journal of Zoology, Volume 24, pp. 331-340.

Jonsson, N., Hansen, L. P. & Jonsson, B., 1991. Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. Journal of Animal Ecology, Volume 60, pp. 937-947.

Jonsson, N., Jonsson, B., Aass, P. & Hansen, L.P., 1995. Brown trout *Salmo trutta* released to support recreational fishing in a Norwegian fjord. Journal of Fish Biology, Volume 46, pp. 70–84.

Jonsson, N. & Jonsson, B., 1998. Body composition and energy allocation in the life-history stages of brown trout. Journal of Fish Biology, Volume 53, pp. 1306-1316.

Jonsson, N. & Jonsson, B., 1999. Trade-off between egg mass and egg number in brown trout. Journal of Fish Biology, Volume 55, pp. 767-783.

Jonsson, N. & Jonsson, B., 2002. Migration of anadromous brown trout in a Norwegian river. Freshwater Biology, 47(8), pp. 1391-1401.

Kennedy, G. J. A. & Greer, J. E., 1988. Predation by cormorants, *Phalacrocorax carbo* (L.), on the salmonid populations of an Irish river. Aquaculture and Fisheries Management, Volume 19, pp. 159-170.

Kerr, S., Kirkpatrick, C., Greer, R. B., Hammar, J. & Skold, E., 2002. Lost last strong hold of Arctic char in Orkney; Heldale Water of Hoy, surveyed by char fanatics. Paper presented at 10th Workshop of the International Society Of Arctic Char Fanatics, Killarney, Ireland, 2/09/02 - 9/09/02, pp. 7-14.

Kirby, P., 2012. Orkney sea trout burns - invertebrate sampling 2011. A report for the Scapa Flow Landscape Partnership.

Kurokawa, T., 1990. Influence of the date and body size at smoltification and subsequent growth rate and photoperiod on desmoltification in under-yearling masu salmon (*Oncorhynchus masou*). Aquaculture, Volume 86, pp. 209-218.

L'Abée-Lund, J.H., 1991. Variation within and between rivers in adult size and sea age at maturity of anadromous brown trout, *Salmo trutta*. Canadian Journal of Fisheries and Aquatic Sciences, Volume 48, pp. 1015–21.

L'Abée-Lund, J. H., Jensen, A. J. & Johnsen, B. O., 1990. Interpopulation variation in male parr maturation of anadromous brown trout (*Salmo trutta*) in Norway. Canadian Journal of Zoology, Volume 68, pp. 1983-1987.

L'Abée-Lund, J. H., Jonsson, B. & Jensen, A. J., 1989. Latitudinal variation in life history characteristics of sea-run migrant brown trout *Salmo trutta*. Journal of Animal Ecology, Volume 58, pp. 525-542.

Laikre, L., Järvi, T., Johansson, L., Palm, S., Rubin, J-F., Glimsäter, C. E., Landergren, P. & Ryman, N., 2002. Spatial and temporal population structure of sea trout at the Island of Gotland, Sweden, delineated from mitochondrial DNA. Journal of Fish Biology, Volume 60, pp. 49–71.

Landergren, P., 2001. Survival and growth of sea trout parr in fresh and brackish water. Journal of Fish Biology, Volume 58, pp. 591-593.

Landergren, P., 2004. Factors affecting early migration of sea trout *Salmo trutta* parr to brackish water. Fisheries Research, Volume 67, pp. 283–294.

Landergren, P. & Vallin, L., 1998. Spawning sea trout, *Salmo trutta* L., in brackish waters - lost effort or successful strategy? Fisheries Research, Volume 35, pp. 229-236.

Laughton, R., 2010a. Rotary Screw Trap Data from the River Tromie 2009-2010, Knockando: Spey Foundation.

Laughton, R., 2010b. Rotary Screw Trap Data from the River Truim 2010, Knockando: Spey Foundation.

Laughton, R., Burns, S., Reid, J. & Miele, R., 2008. The Operation of Rotary Screw Traps in the River Spey 2008. Knockando: Spey Foundation.

Le Cren, E. D., 1973. The population dynamics of young trout (*Salmo trutta*) in relation to density and territorial behaviour. Rapport et Procés-Verbause des Réunions. Conseil International pour l'Exploration de la Mer, Volume 164, pp. 241-246.

Lea, E., 1910. On the methods used in herring investigations. ICES Publication de Circonstane, Volume 53, pp. 7-174.

Lee, R. M., 1912. An investigation into the methods of growth determination in fishes by means of scales. Conseil permanent international pour l'exploration de la mer, Volume 63, pp. 3-35.

Limburg, K. E., Landergren, P., Westin, L., Elfman, M. & Kristiansson, P., 2001. Flexible modes of anadromy in Baltic sea trout: making the most of marginal spawning streams. Journal of Fish Biology, Volume 59, pp. 682-695.

Linklater, E., 2002. Udal Law - Past, Present & Future? LLB (Hons) European Law Dissertation. Glasgow: University of Strathclyde.

Linneaus, C., 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis 1. 10th ed. Stockholm: Laurentius Salvius.

Lundberg, P., 1988. The evolution of partial migration in birds. Trends in Ecology and. Evolution. Volume 3, pp. 172–5.

Maisse, G. & Bagliniere, J. L., 1991. Biology of the brown trout (*Salmo trutta* L.) in French rivers. In: Biology and Ecology of the Brown and Sea Trout. Chichester: Praxis Publishing, pp. 1-15.

Marine Scotland Science, 2010. Shieldaig Project review June 2008 to December 2009. Edinburgh: Marine Scotland.

Marine Scotland, 2012. Sea trout fishery statistics - 2011 season. Montrose: Marine Scotland.

Matthews, M. A., Poole, W. R., Dillane, M. G. & Whelan, K. F., 1997. Juvenile recruitment and smolt output of brown trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) from a lacustrine system in western Ireland. Fisheries Research, Volume 31, pp. 19-37.

McKibbon, M. & Hay, D., 2002. Sheildaig Project Review: June 2001 - June 2002. Aberdeen: Fisheries Research Services.

McKibben, M. & Hay, D., 2004. Shieldaig Project Review: June 2003 - June 2004. Aberdeen: Fisheries Research Services.

MFSTP, 2011. The Moray Firth Sea Trout Project. Final Report. Forres: Moray Firth Sea Trout Project.

Mills, D., 1989. Ecology and management of Atlantic salmon. London: Chapman & Hall, pp. 1-351.

Milner, N. J., Harris, G. S., Gargan, P., Beveridge, M., Pawson, M. G., Walker, A. & Whelan, K., 2006. Perspectives on sea trout science and management. In: G. M. N. Harris, ed. Sea Trout: Biology, Conservation and Management. Proceedings of the First International Sea Trout Symposium, Cardiff, July 2004. Oxford: Blackwell Publishing Ltd, pp. 480-490.

MLURI, 1993. Land Cover of Scotland Database. Executive Summary. Aberdeen: Macaulay Land Use Research Institute.

Moore, A. & Scott, A., 1988. Observations of recently emerged sea trout, *Salmo trutta* L., fry in a chalk stream, using a low-light underwater camera. Journal of Fish Biology, 33(6), pp. 959–960.

Morita, K. & Nagasawa, T., 2010. Latitudinal variation in the growth and maturation of masu salmon (*Oncorhynchus masou*) parr. Canadian Journal of Fisheries and Aquatic Sciences, Volume 67(6): pp. 955-965.

Morrison, B. R. S., 1989. The growth of juvenile Atlantic salmon, Salmo salar L., and brown trout, *Salmo trutta* L., in a Scottish river system subject to cooling-water discharge. Journal of Fish Biology, 35(4), pp. 539-556.

Mortensen, E., 1977. Population, survival, growth and production of trout *Salmo trutta* in a small Danish stream. OIKOS, Volume 28, pp. 9-15.

Mortensen, E., Geertz-Hansen, P. & Marcus, E., 1988. The significance of temperature and food as factors affecting the growth of brown trout, *Salmo trutta* L., in four Danish streams. Polskie Archiwum Hydrobiologii, 35(3-4), pp. 533-544.

Nall, G. H., 1930. The Life of the Sea Trout. London: Seeley, Sevice & Co. Ltd..

Nall, G. H., 1933. Orkney Sea Trout, Edinburgh: HMSO.

NASCO, 2014. Atlantic salmon rivers database [online], available: http://www.nasco.int/RiversDatabase.aspx [accessed 1st June 104].

Neilsen, C., Aarestrup, K., Norum, U. & Madsen, S. S., 2003. Pre-migratory differentiation of wild brown trout into migrant and resident individuals. Journal of Fish Biology, Volume 63, pp. 1184-1196.

Nicieza, A. G. & Braña, F., 1991. Development of length-bimodality and smolting in wild stocks of Atlantic salmon, *Salmo salar* L., under different growth conditions. Journal of Fish Biology, Volume 38, pp. 509-523.

Nicieza, A. G. & Braña, F., 1993. Relationships among smolt size, marine growth and sea age at maturity of Atlantic salmon (*Salmo salar*) in northern Spain. Canadian Journal of Fisheries and Aquatic Sciences, 50(8), pp. 1632-1640.

Nicieza, A. G. & Metcalfe, N. B., 1997. Growth compensation in juvenile Atlantic salmon: responses to depressed temperature and food availability. Ecology, Volume 78, pp. 2385-2400.

Nordeng, H., 1961. On the biology of char (*Salmo alpinus* L.) in Salangen, North Norway. I. Age and spawning frequency determined from scales and otoliths. Norwegian Journal of Zoology, Volume 10, pp. 67–123.

Northcote, T. G., 1978. Migratory strategies and production in freshwater fishes. In: S. D. Gerking, ed. Ecology of Freshwater Fish Production. Oxford: Blackwell Science Publications, pp. 326-359.

OHFT, 2007. Freshwater Fish and Fisheries in the Outer Hebrides: Fisheries Management Plan. Marybank, Lewis: Outer Hebrides Fisheries Trust.

Ohms, H.A., Sloat, M.R., Reeves, G.H., Jordan, C.E. & Dunham, J.B., 2007. Influence of sex, migration distance, and latitude on life history expression in steelhead and rainbow trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences, Volume 71(1): pp. 70-80.

Økland, F., Jonsson, B., Jensen, A. J. & Hansen, L. P., 1993. Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon? Journal of Fish Biology, Volume 42, pp. 541-550.

OTFA, 2010. Orkney's Wild Sea Trout. A report prepared by the Orkney Trout Fishing Association.

OTFA, 2014. Hatchery update 2013/14 [online], available: http://www.orkneytroutfishing.co.uk/hatchery/hatchery_annual_report.html [accessed 1st June 2014]/

Páez D.J., Brisson-Bonenfant, C., Rossignol, O., Guderley, H.E., Bernatchez, L. & Dodson J.J., 2011. Alternative developmental pathways and the propensity to migrate: a case study in the Atlantic salmon. Journal of Evolutionary Biology, Volume 24(2), pp. 245-55.

Pemberton, R., 1976. Sea trout in North Argyll sea lochs. 2. Diet. Journal of Fish Biology, Volume 9, pp. 157-179.

Pettersson, J.C.E., Hansen, M.M. & Bohlin, T., 2001. Does dispersal from landlocked trout explain the coexistence of resident and migratory trout females in a small stream? Journal of Fish Biology, Volume 58, pp. 487–95.

Piché J., Hutchings, J.A. & Blanchard, W., 2008. Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*. Proceedings of the Royal Society B: Biological Sciences, Volume 275, pp. 1571-1575.

Pickering, A. D., Pottinger, T. G. & Christie, P., 1982. Recovery of the brown trout, *Salmo trutta* L., from acute handling stress: a time course study. Journal of Fish Biology, 20(2), pp. 229-244.

Pratten, D. J. & Shearer, W. M., 1983a. Sea trout of the North Esk. Fisheries Management, 14(2), pp. 49-65.

Pratten, D. J. & Shearer, W. M., 1983b. The Migrations of North Esk Sea Trout. Fisheries Management, 14(3), pp. 99-113.

Raffell, J., Buttle, S. & Hay, D., 2007. Shieldaig Project Review June 2006 - June 2007, Aberdeen: Fisheries Research Services.

RAFTS, 2012. Report and financial statements for the year ended December 31st 2011.

Rasmussen, G., 1986. The population dynamics of brown trout (*Salmo trutta* L.) in relation to year-class size. Polskie Archiwum Hydrobiologii, Volume 33, pp. 433-453.

Rasmussen, G. H., 2006. Research Activities and Management of Brown Trout and Sea Trout (*Salmo trutta* L.) in Denmark. In: G. Harris & M. N, eds. Sea Trout: Biology, Conservation and Management. Proceedings of the First International Sea Trout Symposium, Cardiff, July 2004. Oxford: Blackwell Publishing, pp. 342-348.

Regan, C. T., 1911. The freshwater fishes of the British Isles. London: Meuthen and Co.

Ricker, W., 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada, Volume 11, pp. 559-623.

Roff, D.A., 1996. The evolution of threshold traits in animals. Quarterly Review of Biology, Volume 71, pp. 3-35.

Roper, B. B. & Scarneccia, D. L., 1999. Emigration of age-0 chinook salmon (*Onchorhynchus tshawytscha*) smolts from the upper South Umpqua River basin, Oregon, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences, 56(6), pp. 939-946.

Rossignol, O., Dodson, J.J. & Guderley, H., 2011. Relationship between metabolism, sex and reproductive tactics in young Atlantic salmon. Comparative Biochemistry and Physiology A: Molecular and Integrative Physiology, Volume 159, pp. 82-91.

Rubin, J.-F., Glimsäter, C. & Jarvi, T., 2005. Spawning characteristics of the anadromous brown trout in a small Swedish stream. Journal of Fish Biology, Volume 66, pp. 107–121.

Saunders, R. L. & Radway Allen, K., 1967. Effects of tagging and fin-clipping on the survival and growth of Atlantic salmon between smolt and adult stages. Journal of the Fisheries Research Board of Canada, 24(12), pp. 2595-2611.

SEPA, 2014. Small water bodies in Orkney [online], available: http://www.sepa.org.uk/water/river_basin_planning/area_advisory_groups/orkney_and_shetland/small_water_bodies_in_orkney.aspx [accessed 1st June 2014].

SFCC, 2007. Electrofishing team leader training manual. Fisheries management SVQ Level 3: Manage Electrofishing Operations. Scottish Fisheries C-ordination Centre. Inverness: Inverness College

Shackley, P. E. & Donaghy, M. J., 1992. The Distribution and Growth of Juvenile Salmon and Trout in the Major Tributaries of the River Dee Catchment (Grampian Region). Pitlochry: Freshwater Fisheries Laboratory, Scottish Office Agriculture and Fisheries Department.

Shrimpton, J.M., Björnsson, B.Th., McCormick, S.D., 2000. Can Atlantic salmon smolt twice? Endocrine and biochemical changes during smolting. Canadian Journal of Fisheries & Aquatic Sciences, Volume 57, pp. 1969–1976.

Skoglund, H., & Barlaup, B.T., 2006. Feeding pattern and diet of first feeding brown trout fry under natural conditions. Journal of Fish Biology, Volume 68(2): pp. 507-521.

SNH, 2001. Natural Heritage Zones: a National Assessment of Scotland's Freshwaters. Perth: Scottish Natural Heritage.

Soivio, A., Myllynen, K., Pakkala, J. & Jokela, S., 1998. Smolting of the brown trout *(Salmo trutta* L.) in Lestijoki water. Boreal Environment Research, Volume 3, pp. 387-393.

Solbé, J., 1988. Water quality for salmon and trout. Pitlochry: Atlantic Salmon Trust.

Solomon, D. J., 1995. Sea trout stocks in England and Wales. R&D Report 25. Bristol: National Rivers Authority.

Spence, M., 1914. Flora Orcadensis: containing the flowering plants arranged according to the natural orders. Kirkwall: D. Spence.

SQW Ltd, 2006. Assessing the value and realising the potential of sustainable freshwater fisheries in Orkney. Scottish Natural Heritage Commissioned Report No. 156 (ROAME No F04LA09).

Stefansson, S. O., McGinnity, P., Björnsson, B. T., Schreck, C. B. & McCormick, S. D., 2003. The importance of smolt development to salmon conservation, culture and management: perspectives from the 6th International Workshop on Salmonid Smoltification. Aquaculture, Volume 222, pp. 1-14.

Stefansson, S. O., Björnsson, B. T., Ebbesson, L. O. E. & McCormick, S. D., 2008. Smoltification. In: R. N. Finn & B. G. Kapoor, eds. Fish Larval Physiology. New Delhi: Science Publishers, Inc. Enfield (NH) & IBH Publishing Co. Pvt. Ltd, pp. 639-681.

Svendsen, J. C., Koed, A. & Aarestrup, K., 2004. Factors influencing the spawning migration of female anadromous brown trout. Journal of Fish Biology, 64(2), pp. 528-540.

Swingland, I.R., 1983. Intraspecific differences in movement. In: Swingland, I.R. and Greenwood, P.J., eds. The Ecology of Animal Movement. Oxford: Clarendon Press, pp. 102–15.

Tanguy, J.M., Ombredane, D., Baglinière, J.L. & Prunet, P., 1994. Aspects of parr smolt transformation in anadromous and resident forms of brown trout (*Salmo trutta*) in comparison with Atlantic salmon (*Salmo salar*). Aquaculture, Volume 121, pp. 51–63.

Thériault, V., Bernatchez, L. & Dodson, J.J., 2007. Mating system and individual reproductive success of sympatric anadromous and resident brook charr, Salvelinus fontinalis, under natural conditions. Behavioral Ecology and Sociobiology, Volume 62 (1): pp. 51-65.

Thériault, V. & Dodson, J.J., 2003. Body size and the adoption of a migratory tactic in brook charr. Journal of Fish Biology, Volume: 63(5): pp. 1144-1159.

Thériault, V., Garant, D., Bernatchez, L. & Dodson, J.J., 2007. Heritability of life-history tactics and genetic correlation with body size in a natural population of brook charr (*Salvelinus fontinalis*). Journal of Evolutionary Biology, Volume 20 (6), pp. 2266–2277.

Thomson, M., 2010. Survey of migratory salmonid populations in the Gossa Water, Yell, Shetland. Stromness: SULA Diving.

Thorpe, J.E., Mangel, M., Metcalfe, N.B. & Huntingford, F.A., 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology, Volume 12, pp. 581–99.

Titus, R. G. & Mosegaard, H., 1989. Smolting at age 1 and its adaptive significance for migratory trout, *Salmo trutta* L., in a small Baltic coast stream. Journal of Fish Biology, Volume 35 (Supplement A), pp. 351-353.

Titus, R. G. & Mosegaard, H., 1992. Fluctuating recruitment and variable life history of migratory brown trout, *Salmo trutta* L., in a small unstable stream. Journal of Fish Biology, Volume 41, pp. 239-255.

Toledo, M. M., Lemaire, A. L., Baglinière, J. L. & Braña, F., 1993. Biological characteristics of sea trout (*Salmo trutta* L.) in northern Spain, in two rivers of Asturias. Bulletin Francais de al Peche et de la Pisciculture, Volume 330, pp. 295-306.

Turnpenny, A. W. H. & Williams, R., 1980. Effects of sedimentation on the gravels of an industrial river system. Journal of Fish Biology, Volume 17, pp. 681-693.

Tweed Foundation, 2010. The fishes of the Tweed and the Eye. A2: Sea Trout and Brown trout. Melrose: The Tweed Foundation.

UKHO, 2012. North of Scotland Pilot (Admiralty, Sailing Directions). 8th ed. Taunton: United Kingdom Hydrographic Office.

Vollestad, L. A. O. E. M. & Forseth, T., 2002. Growth-rate variation in brown trout in small neighbouring streams: evidence for density-dependence? Journal of Fish Biology, 61(6), pp. 1513-1527.

Walker, A. F., 1987. The sea trout and brown trout of the River Tay. In: M. J. Picken & W. M. Shearer, eds. Sea Trout in Scotland. Oban: Scottish Marine Biological Association and the Department of Agriculture and Fisheries for Scotland.

Watt, J., 2008. Viking Baseline Assessment of Fish Populations. Arisaig: Waterside Ecology.

Webb, J., Youngson, A. & Verspoor, E., 2009. Restoration guidance for west coast salmon and sea trout fisheries. Edinburgh: Tripartite Working Group.

Went, A. E. J., 1938. Salmon of the River Shannon. I. Analysis of the Stock of 1927. II. Growth of Salmon Smolts in the River Shannon. Proceedings of the Royal Irish Academy, Volume 44 (B), pp. 261-322

Went, A. E. J., 1949. Sea trout of the Owengowla (Gowla River). Sci. Proc. R. Dublin Soc. Volume 1A (No. 10), pp. 265-296.

Went, A. E. J., 1962. Irish sea trout, a review of investigations to date. Scientific Proceedings of the Royal Dublin Society, 1A(10), pp. 265-296.

West-Eberhard, M. J., 2003. Developmental Plasticity and Evolution. New York: Oxford University Press.

Wester Ross Fisheries Trust, 2001. Annual Review 2001. Gairloch: Wester Ross Fisheries Trust.

Wester Ross Fisheries Trust, 2010. Available at: http://www.wrft.org.uk [Accessed 20 June 2011].

Wester Ross Fisheries Trust, 2013. Annual Review 2013. Gairloch: Wester Ross Fisheries Trust.

Westley, P.A.H., Stanley, R., Fleming, I.A., 2013. Experimental Tests for Heritable Morphological Color Plasticity in Non-Native Brown Trout (*Salmo trutta*) Populations. PLoS ONE Volume 8(11): e80401. doi:10.1371/journal.pone.0080401.

Whelan, K.F., 2014. Sea-trout populations in small coastal streams. Biology and Environment: Proceedings of the Royal Irish Academy, Volume 114B (3), pp. 199-204.

Wysujack, K., Greenberg, L.A., Bergman, E. & Olsson, I.C., 2009. The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. Ecology of Freshwater Fish, Volume 18 (1), pp. 52–59.

Youngson, A. F., Jordan, W. C., Verspoor, E., McGinnity, P., Cross, T. & Ferguson, A., 2003. Management of salmonid fisheries in the British Isles: towards a practical approach based on population genetics. Fisheries Research, 62(2), pp. 193-209.